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Proceedings of the

**TENTH  
INTERNATIONAL  
CONGRESS OF  
ENTOMOLOGY**

MONTREAL, AUGUST 17-25, 1956

Managing Editor — Edward C. Becker

Published—December 1958

volume **4**

STORED PRODUCTS ENTOMOLOGY  
FOREST ENTOMOLOGY  
BIOLOGICAL CONTROL  
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# THE CONGRESS INSECT

The illustration on the cover is *Grylloblatta campodeiformis*, an insect discovered near Banff, Alberta, in 1913, by Dr. E. M. Walker, Emeritus Professor of Zoology at the University of Toronto and an Honorary Vice-President of this Congress. It is, perhaps, from the anatomical or phyletic standpoint, the most remarkable of Canadian insects. In a general sense an orthopteroid, it shows resemblances both to the Saltatoria and to the Blattaria and, together with a more recently discovered Japanese genus, ranks as an independent suborder or order.

*Grylloblatta* is adapted to cold conditions. It is found in the Rocky Mountains, near the timberline, living in decaying wood or moss among loose rock. It feeds on other insects and is nocturnal in habits.

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**INDEX**

	Pages
General Papers . . . . .	5-106



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# The Control of Infestation in Stored Products Moving in International Trade

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## ABSTRACT

Countries dependent on the import of a substantial part of their human and animal food and industrial raw materials, have hitherto tolerated excessive levels of infestation in such imports. Importers, processors and consumers are showing increased resistance to receiving infested commodities, especially as educational and advisory work shows the trading community that infestation is not inevitable and that control measures can and ought to be applied in countries of origin.

The principal hazards of infestation are described as well as methods — such as inspection, grading and compulsory fumigation — which can be applied in producer countries to ensure that goods are shipped free from infestation, apparent or hidden.

The extent to which infestation develops during ocean voyages in goods already infested when loaded, from residual infestations in the holds of ships, and by movement of insects from one commodity to another is examined. The need for inspection and treatment of the holds of ships is stressed and some attention is given to the legal aspects of infestations of cargoes. The need for research on the ecological conditions in ships' holds is emphasized.

The importer objects to receiving infested stocks for the two main reasons of difficulty of further conservation and of contamination, and the plant health officer to the possible introduction of new field crop pests. A possible difference of attitude between the trader in commodities and the processor is discussed. The methods of defence which can be used by an importing country are described, with special reference to their quantitative limitations, to regulatory aspects, to international co-operation, and to the need for education of the commercial community.

## INTRODUCTION

There is a tendency to regard the entomology of stored products as being primarily concerned with long term storage, and for the day by day problems concerned in the movement and processing of stored products to receive less attention than they merit. In this paper I intend to direct attention to certain of these problems, especially those most closely concerned with the movement of susceptible commodities in international trade. These are of particular importance to a country such as the United Kingdom, which imports the major part of its foodstuffs and raw materials from many parts of the world.

In this paper I am mainly concerned with the conditions and fate of commodities during transport to consumer countries and after their import. Conditions of storage within producer countries are of interest in so far as they affect the extent of infestation in, and the quality of, goods at time of export.

The importer has two main interests. On the one hand he requires goods which can be stored safely and which, whilst needing protection from indigenous warehouse pests, do not bring with them other pests which will breed and cause damage and loss. This is particularly important for seasonal goods and for reserve stocks. On the other hand there is an increasing objection to the mere presence of insects, by processors, consumers, and public health officials. The whole sequence of events from farm to consumer forms a part of a continuous process, needing, at each stage, a different form of protection from insects and mites. The problems of infestation in international trade could be largely solved if producer countries would establish proper organisations for ensuring that all susceptible commodities are substantially free from infestation at time of export and are loaded into clean ships. Importing countries will require to maintain their own defensive organisations, but the extent of action necessary will be reduced to a minimum if international movement of badly infested commodities can be prevented.

## PROBLEMS OF THE EXPORTING COUNTRY

GENERAL CONSIDERATIONS: The ability of exporting countries to deliver pest free produce at their ports depends primarily on the attention given to the conservation of crops and to the products manufactured from them. There are few parts of the world where raw or processed agricultural products will remain safe from attack by insects or mites indefinitely, without proper protection.

The amount of care necessary increases generally from temperate to tropical regions, but extremes of climate alone provide no natural protection. Surveys by entomologists of the Canadian Department of Agriculture have shown that the rusty grain beetle, *Cryptolestes ferrugineus* (Steph.), occurs on farms in Canada to the northern limits of grain growing, with sub-zero temperatures for many months in the winter; this species may cause heating even during winter in large bulks of grain; the Indian meal moth, *Plodia interpunctella* (Hübner), is a serious pest of seed wheat in Morocco, in inland centres where temperatures are high and humidities very low during the summer; and the khapra beetle, *Trogoderma granarium* (Everts), is the only species which can reproduce during the dry season under extremely hot and dry conditions found at the surface of piles of grain in the Sudan (Oxley, 1950) and pyramids of groundnuts in Northern Nigeria (Howe 1952).

In all climatic zones between these extremes different species of insects are adapted to survival and reproduction, so that no area can be regarded as safe. Thus the Australian spider beetle, *Ptinus tectus* (Boiel.), needs relatively mild and humid conditions (Howe and Burges, 1953) whereas the adult hairy spider beetle, *Ptinus villiger* (Reitt.), must be exposed to a period of very low temperature during the winter for successful breeding during the following summer (Howe and Burges, 1955). For the United States (Walkden *et al.*, 1953) and Turkey charts have been issued showing the zones of grain storage within which varying risks of infestation and damage during one year's storage may occur.

FIELD INFESTATION: A particular hazard of the warmer regions is that of field infestation by storage pests. In most temperate countries one can assume that crops first become infested by insects after they have entered a storage building or container (e.g. sack or lorry). A prevention and control programme constructed on that assumption may fail in the tropics if the crop is already infested in the field.

Field infestation falls into two categories. The first is that by insects which are essentially field pests, but which complete their development in the dried seeds. Examples are the pea beetle (weevil), *Bruchus bisorum* (L.), and the lentil beetle, *Bruchus ervi* (Froel.), which develop on the growing pea and emerge after harvest. Other species of Bruchids may attack in the field but are also capable of continuing to breed in the dried pulses in store. These include *Acanthoscelides obtectus* (Say) and *Callosobruchus chinensis* (L.). Another example is the moth, *Ephestia figulilella* (Greg.) which is stated to attack ripening raisin grapes in California, to complete development in the dried fruit but to be replaced in older fruit by *Plodia interpunctella* (Hbn.) and by *Oryzaephilus surinamensis* (L.) (Simmons and Donohoe, 1938).

The second category is that of field infestation by true storage insects. These do not necessarily remain outside throughout the year but fly to fields of ripening grain from nearby grain stores; the insects principally concerned are *Calandra oryzae* (L.) and *Sitotroga cerealella* (Oliv.). The problem is most serious with maize, especially where it is allowed to stand drying in the fields until the farmer finds it convenient to harvest. In the S.E. United States *Calandra oryzae* is regarded as one of the major field pests of maize. Rapid harvesting of grain by combine is said to have reduced the incidence of attack in the field by *Sitotroga* in wheat and rice in the U.S.A. For export crops every effort should be made to prevent field infestation, since larvae within seeds are difficult to detect by normal inspection methods, and commodities apparently free from infestation but actually infested may be exported as sound, to the detriment of the reputation of the exporting country.

QUALITY CONTROL: There is considerable variation from one exporting country to another in the extent to which measures are taken to check the quality of goods at time of shipment. In the long run such action is based on the demands of

purchasers and the extent of competition for export markets. One early example of the influence of customers was seen in 1929, when severe infestation of Rhodesian tobacco by *Ephestia elutella* (Hübner) occurred in stocks lying in London (Bovingdon, 1933). When widespread infestation by this moth was found in tobacco barns and sheds in Southern Rhodesia, legislation was immediately passed to provide for compulsory measures of control. This was done to preserve the valuable preferential United Kingdom market (S. Rhodesia, 1931).

One of the major recent influences has been the import requirements of the U.S.A. Food and Drug Administration (F.D.A., 1947) and of individual European importers. Another example is that of Venezuela which insists on certificates of freedom from infestation for all imports of flour. So far as Canada is concerned, these certificates are only issued on the basis of regular official inspection and licensing of flour mills wishing to export. In some countries the necessary measures are taken by Government organisations, whereas in others nothing official is done, individual exporters being left free to export goods in any condition they please. A combination of the two can commonly be found, where, for example, strict regulations apply to commodities which are officially graded, whereas other ungraded goods are subject to no regulations at all and may even be shipped in the same vessels as the graded goods.

The measures adopted may be extremely thorough and far reaching, designed to maintain the main export crop in good condition from farm to port. In Canada, for example, this is done by the grain grading system, with licensing and regular inspection of elevators by Dominion government officials and the application of strict sanctions if infestation is discovered (Canada 1930). It should be noted that there is no provision for 'weevily' suffixes in the Canadian grading system, all grain in which living insects are found being degraded until satisfactorily treated.

In the U.S.A. the 'weevily' suffixes provides a slight toleration for living "weevils"<sup>1</sup> (in practice about 2 weevils per kilogram), but prevent the export of badly infested graded grain (U.S.D.A., 1952).

Other countries, Australia and Argentina, for example, which export grain on an F.A.Q. basis, have no official tolerances for living insects, although the amount of insect damage is limited for normal quality grain exported from the latter (Argentina, 1951). In Morocco, however, exports of wheat and common barley, for example, are subject to a tolerance of two weevils per kilogram, although the grain is sold on an F.A.Q. basis (Morocco, 1953). Difficulties in the marketing of pulses, owing to the obvious damage done by Bruchid beetles, has led to many exporting countries laying down strict standards for damage and presence of adult beetles.

One aspect of infestation as a factor in grading or quality control schemes should be criticised at this point. In the grading systems known to me, infestation is judged by the presence or absence of living adult insects and damage by obvious holes. The same criteria are used in the examination of commercial samples. The "adult insect" criterion has a number of disadvantages. Grain or pulse which is infested by internal feeding insects may be graded as sound because the adults may not have emerged, or they may have been screened or aspirated out before inspection, or the material may have been fumigated at a low dosage and for a period too short to kill immature stages. Certificates may be issued in good faith showing products to be free from insects at time of inspection, but the commodity may arrive at its destination in the importing country badly infested and damaged, because of the development of hidden infestation on the voyage. The importer or the shipowner may have no redress against the exporter because of the certificate. In the United States wheat may be graded free from weevils under this system but may be refused by the flour miller, who, examining the grain with X-ray machines, may find larval forms in such numbers as to make it impossible for him to mill a flour sufficiently free from insect fragments to satisfy the pure food laws.

One method of avoiding the need for tolerances of living insects is for countries to prescribe compulsory fumigation or other treatment for all or certain kinds of exports. Such compulsory fumigation may be prescribed for some or all of certain kinds of exports. Thus the Brazilian Plant Protection legislation requires fumigation of all export maize, pulses, and cottonseed, but not cocoa beans; Algeria requires

<sup>1</sup>"Weevils" are defined as *Calandra granaria* (L.), *C. oryzae* (L.) and *Rhyzopertha dominica* (Fab.). *Sitotroga cerealella* (Oliv.) is taken into account during inspection of the bulk but not during the examination of samples.



fumigation of pulses, dates and figs, but other commodities such as wheat bran and carobs are not regulated. Limitations may be placed on date of shipment after harvest, to reduce risk of infestation and development of insect damage during storage. Thus no figs may be exported from Greece to the U.S.A. after the end of September.

Apart from Government requirements many exporters have found it commercially necessary to treat goods before export, so as to satisfy their overseas customers. Fumigation is done for currants from Greece for the U.S.A., for walnuts from India and France for Europe and the U.S.A., for groundnuts from S. Africa for all destinations, and for wheat from Turkey. Madagascar beans and beans from E. Africa are treated with inert dusts or with those containing lindane.

The actual techniques of fumigation at time of export range from the use of elaborate vacuum or atmospheric fumigation chambers—as in N. Africa and the United States; to the use of gas proof sheets on goods *in situ* in dock sheds, as in S. Africa, or even treatment in the loaded holds of ships, as in Brazil. Grain may be treated in conventional silos using calcium cyanide, halogenated hydrocarbons or methyl bromide. Treatment is quicker and more effective in silos fitted with circulatory fumigation apparatus, as in Tunisia and Turkey. It is important that the methods should be reasonably fast, effective, and economical and should interfere as little as possible with the normal flow of trade.

**INFESTATION OF TRANSPORT VEHICLES AND TRANSIT SHEDS:** In exporting countries infestation may occur at all stages from farm to port, including premises such as flour mills and oilseed crushing plants, in which raw agricultural products are processed. Two aspects are of particular importance. Transport vehicles may have residual infestations which maintain themselves in spillage. In the U.S.A., special studies have been made of this problem and a number of railway box cars have been fitted with compressed glass wool blocks to fill up spaces behind the end bulkheads. Infestation in such “weevil test” cars has been much reduced (MacSpadden, 1955). In Argentina all transport used for carriage of grain and grain products, oilseeds and oilseed products must be treated before and after use with a DDT/BHC dust (Argentina, 1953). General infestations in elevators can cause grain to be infested in a manner not detected by normal grading inspections. It is of little use to fumigate commodities if these are then liable to be reinfested by being stowed near other infested goods in transit sheds.

## PROBLEMS OF TRANSPORT BY SEA

**GENERAL CONSIDERATIONS:** The carriage of infested goods from one country to another in ships has been the principal means by which most storage pests have been distributed. This has occurred not only directly but also indirectly through the survival of insects and mites in residues in ships’ holds. Adult beetles can remain alive for long periods without food and some insect larvae will pass into diapause. Thus during May 1956 it was observed, in a ship on regular voyages between the Mediterranean and U.K. ports, that larvae of *Aphomia gularis* (Zell.) were pupating. These larvae had migrated into a wooden bulkhead from a cargo of rice carried in September 1955. Locally heated places in ships, especially near engine room bulkheads, in casings surrounding steam pipes, and the propellor shaft tunnel, enable insects to survive and continue breeding during voyages when conditions in other parts of the holds are likely to be lethal.

The second main source of infestation is movement of insects from one commodity to another in the same or different holds during the voyage or during loading and unloading. Many examples in both these categories are given by Freeman (1948, 1950) and Monro (1951).

The problems of infestation associated with the carriage of goods by sea may be considered under the two broad headings of infestation in holds and infestation in cargoes.

**INFESTATION IN HOLDS:** The problem of keeping holds free from infestation is most simple for ships on regular runs carrying whole cargoes of relatively uninfested commodities, e.g., U.S.A./Canada — Great Britain, but even here the most unexpected and sometimes inexplicable residual infestations have been found from time to time.



It is most difficult for ships engaged in voyages, particularly in the tropics, where they call at many ports, loading and unloading small quantities of infested commodities, and are rarely entirely empty. The question can be examined from three aspects; contractual, statutory and technical.

The charter parties under which ships are hired may often include terms relating to infestation. Thus time charters not infrequently include a clause providing that the owners shall pay fumigation costs within the first six months of the charter, unless it can be shown that the infestation for which the fumigation is necessary results from cargo carried during that period.

Generally all contracts in respect of shipment of cargoes are subject to the Hague Rules of 1921, which are incorporated into the terms of bills of lading or required by national legislation. Under these rules a shipowner is bound to provide a ship which is not only seaworthy but also cargo-worthy. The presence of weevils or other insects remaining in the holds after discharge of a previous cargo could be regarded as violating this obligation, if the ship was presented for loading a fresh cargo.

In practice there may be great difficulty in making sure that the cargo space is in fact free from residual infestation. For this purpose a cargo owner may employ cargo superintendents or marine surveyors, but this is not always possible and in any event these men may lack the necessary special knowledge and experience for entomological inspection. A cargo owner therefore may have the greatest difficulty in proving a claim for infestation caused by a dirty ship. However shipowners usually cover themselves against such liabilities by insurance or, more commonly, by entering their ships in mutual protecting and indemnity clubs. It is these clubs which normally undertake the defence of shipowners against claims and which are likely to be interested in measures to reduce or eliminate them.

Certain countries carry out official inspection of empty holds for infestation before loading is permitted. In Canada inspectors of the Plant Protection Division of the Department of Agriculture have the power to inspect ships which are to carry cereal exports, including grain or grain products, corn and oilseeds and to require treatment to the extent and in the manner deemed necessary by the inspector (Canada, 1955). In the U.S.A., a licensed grain grading inspector can refuse to grade grain if he considers that the hold into which the grain is to be loaded is in such a condition as to contaminate the grain or lower the grade (United States, 1941). A hold in which storage insects are found is regarded as unfit for loading. The method of treatment is left to the shipowner.

As far as the writer is aware these are the only exporting countries which have such statutory requirements. Of course the system is only really applicable where the produce to be loaded is itself reasonably clear of infestation. As exporting countries raise their standards and decrease infestation in their produce, such inspection and treatment procedures may be established elsewhere.

More could be done to reduce infestation in holds by exchange of information between official services responsible for inspection in exporting and importing countries. This has existed for several years between the respective services in Canada and the United Kingdom and is being developed with the United States. As an example the existence of a residual infestation of *Trogoderma granarium* (Everts) in a ship which could not be treated in the United Kingdom, was notified to the United States Department of Agriculture. This ship was specially inspected on arrival and was fumigated, and no material was landed which might have introduced this species into the Eastern United States.

As technical problems the detection of infestation and the proper cleaning and removal of residues from ships' holds are more difficult than the treatment of residual infestation when discovered. There are many ledges on girders, pipe casings and spaces where dust and cargo debris may settle, which can only be thoroughly inspected and cleaned either when cargo is in the holds or by the use of special scaffolding when they are empty.

Work carried out principally in Canada (Monro *et al.*, 1952) has shown that methyl bromide is the most effective fumigant for treatment of empty holds, but other countries have been slow to use this fumigant and have tended to continue to use hydrogen cyanide. The expense, inconvenience and time needed for fumigation have

influenced shipowners to prefer other methods, such as sprays and smokes. Although these are not so efficient as general hold fumigation they are reasonably effective if combined with thorough cleaning, and are especially useful if the infestation is superficial. The sprays used are generally oil based, the insecticides including pyrethrins-piperonyl butoxide, DDT, gamma BHC, methoxychlor and chlordane. Smokes used are DDT and gamma BHC (lindane) alone or in combination. In Canadian ports methyl bromide fumigation is generally required except for local infestations for which spraying is permitted. Spraying is the method generally employed in U.S.A. ports, fumigation being exceptional. Smokes are particularly recommended in the United Kingdom, although not to the exclusion of fumigation (hydrogen cyanide or methyl bromide) in suitable cases. The shipowner prefers sprays and smokes because they are less expensive, cause little or no delay to the ship, do not involve landing the crew, enable work to proceed in other holds during treatment, and because the treatments may be done at sea during the voyage to the loading port. In the United Kingdom shipowners are encouraged to carry out regular treatments by sprays or smokes. Fumigation is generally regarded as a method to be kept in reserve for treating serious infestations, especially when ships are going to countries where goods are likely to be free from infestation. Such routine smoke or spray treatments are useful where ships are regularly carrying infested commodities, especially when these are loaded and unloaded en route, so that the ship is seldom entirely empty. Much work needs to be done, however, in the critical evaluation of the various methods of control used and in the study of the construction of ships with the object of recommending modifications of design to reduce the number of places in which residues can lodge.

**INFESTATION IN CARGOES:** The disinfection of holds may be futile if the cargo to be loaded is infested. In addition to the possible development of infestation in cargo during the voyage there is the risk of movement of insects from one commodity to another and of insects being left in the holds after discharge of cargo. Cross infestation is particularly important where ships pick up cargo at intermediate points, as for example on the runs between South and East Africa; and the Far East, India, Sudan and the United Kingdom. Produce shipped from one country may be free from infestation, but become contaminated *en voyage* from infested goods loaded at other ports. This may even occur at individual ports where shippers of valuable commodities, such as edible nuts or dried fruit, may arrange for fumigation prior to shipment only to find that their fumigated goods are stowed in with unfumigated and infested goods such as sorghum, maize meal, oilseeds and pulses. This has occurred during 1956 in shipments of ground-nuts from South Africa and India to the United Kingdom, and during 1955 and 1956 in shipments of flour and animal food from the United States.

The problem may be examined in the light of the contractual, legal and technical aspects.

It has already been pointed out that the shipowner is responsible for providing that the holds of a ship are in a fit state for the carriage and preservation of goods and that this infers freedom from infestation. On the other hand the International Rules referred to excuse the shipowner from liability for damage caused by the "inherent vice" of the goods. "Inherent vice" has been defined as "anything which by reason of its own inherent qualities is lost without any negligence by anyone". It may be defined as inability to travel safely under ordinary commercial conditions (Scrutton, 1955 art. 79).

Insect infestation may be regarded as "inherent vice". Thus it has been held, in the course of commercial argument, that a shipowner is not liable for damage to maize as the result of heating caused by insects. The shipowner was not responsible for the insects introduced with the maize, nor could he do anything to arrest their development during the voyage. If the weevils were to infect other cargo in the ship it is considered that the shipowner would have a claim against the owner of the maize for any damages which he might, in the first place, have to pay to the receivers of the other cargo. On the other hand if the cargo was obviously infested at time of loading or was of a type generally known to be infested, the shipowner might be liable under the clauses relating to bad stowage.

A recent development, particularly on the part of certain British shipowners on lines from the Far East and East Africa, has been to refuse to carry such heavily infested commodities as gram, rice, bran, and cowpeas, unless these have first been fumigated. Probably this has occurred as the result of claims from other cargo owners.

The owners of goods may insure themselves under most marine cargo policies, against losses due to infestation discovered in the goods on arrival. This has been especially necessary in recent years for shipments<sup>2</sup> of Australian flour to the United Kingdom and considerable claims have been made under these insurance policies during the past few years, principally because of infestation by *Ephestia cautella* (Walk.). Some insurers have even declined further business. However, insurance does not compensate for all the losses since the importer is often put to considerable trouble in rendering goods fit for sale and his customers, knowing of the infestation, may be prejudiced against his goods in favour of others which arrive uninfested.

When entomologists are asked to give advice on the origin of infestations in goods in ships, they often find themselves in difficulties because of lack of information not only regarding the biology and habits of the insects but also of the detailed history of the goods and of the ship concerned. Another obstacle frequently encountered is the ignorance of elementary biology of many of those concerned with handling the goods with the result that the wrong questions may be asked, sometimes long after the essential evidence has disappeared. A knowledge of the insects and mites which are most likely to occur on commodities of different origin, based on surveys carried out during the discharge of ships, is also very helpful. Importing countries which make such surveys can greatly assist the efforts made in producer countries by making periodical reports on the extent and degree of infestation found.

Information of a general kind has been given in Freeman (1948a, b) and, specially for West Africa, in Howe and Freeman (1955).

Treatment of cargo in the holds of ships presents great difficulties, but some fumigation in the holds of ships has been done in various countries. In the United States of America, bulk grain stored in the lower holds of ships has been fumigated successfully by surface application of chlorinated hydrocarbons. Similar techniques and materials have been used commercially in Turkey, Greece and Pakistan, (Ahmad, 1954) for fumigation of grain cargoes in ships. In Chile, hydrogen cyanide is used, in grain ships, for the control of *Sitotroga cerealella* (Chevez, 1956). In Brazil complete holds loaded with bagged or bulk goods have been fumigated with methyl bromide (Pereira and Andrade, 1952), but the results have not been comparable with those obtained by fumigation on shore, when judged by the extent of infestation in cargo on arrival in the country of destination.

No solution, apart from careful segregation, has yet been developed for the problem of cross infestation from one parcel to another. Very little is known regarding the conditions affecting insect and mite populations in cargo during voyages in various parts of the world. Considerable interest has been taken in the study of humidity changes in holds with the object of reducing damage due to condensation and in the safe carriage of refrigerated cargoes (Colvin and Duly, 1947). Little however appears to have been done in the scientific study of dry cargo, especially of conditions affecting infestation. Some studies were carried out from 1912-1914 on the carrying qualities of maize from the U.S.A. to Europe (Boerner, 1919), and a single study in 1917 of Manitoba wheat from Vancouver to the United Kingdom (Birchard and Alcock, 1918). Duly (1931) gives some figures of changes in temperature of a cargo of wheat during a summer voyage from New Orleans to Hull.

Research is thus needed not only into methods for the treatment of commodities in ships and for the prevention of cross-infestation but also into the ecological conditions affecting insects and mites in ships. For example, shipments of Canadian wheat, passed as clear of infestation in Vancouver, have been found heating and infested with *Cryptolestes ferrugineus* on arrival six weeks later in the United Kingdom. The

<sup>2</sup>Flours "all risks" — "Weevil clause" (applying to Great Britain and Northern Ireland) . . . this (Insurance) Company agrees to reimburse the assured for the actual cost of sifting any sacks of flour, which on arrival prove to be infested by insects, and for actual expense incurred in brushing or reconditioning such sacks, including any necessary and additional expenses incidental to such sifting, brushing and/or reconditioning and for any incidental loss in weight in consequence thereof — but there shall be no liability hereunder for depreciation, loss of market or delay." . . . Notice to be given within 72 hours after discharge.



infestations were confined to those holds with warm bulk-heads or propellor shaft tunnels, i.e., sources of heat (Freeman, 1952, 1953). Such studies are urgently needed and can only properly be done on an international basis with the assistance of shipping companies. Questions of particular importance are the effects on insect populations in bulk cargoes of local sources of ships' heat, the rate of development of infestations, the conditions which affect spread of insects from one commodity to another, and the difference in the environments provided by bulk and bagged commodities.

### PROBLEMS OF THE IMPORTING COUNTRY

GENERAL CONSIDERATIONS: From the point of view of the importing country, there are three main objections to the continued importation of infested commodities. The first is the risk of continued loss and damage to the imported goods by breeding of insects and mites introduced on them. The second is the risk of infestation of other imported goods, of home produced goods, and of warehouses and mills by these insects. The third is the risk of introduction and establishment of new pests. The problems may be considered from the point of view of traders in commodities, users, manufacturers and consumers, and those responsible for general hygienic and phytosanitary measures.

COMMERCIAL ASPECTS: Hitherto in the United Kingdom, many traders in imported commodities have shown little interest in the nature and degree of infestation in their goods. Firstly they usually rely on selling them quickly, some commodities being bought and sold perhaps a dozen times in one day, without the owners having seen the actual goods, which may still be afloat. Secondly they deal in goods on a "fair average quality" or conventional descriptive basis which may include some degree of insect infestation or damage as a normal property of the goods. Such traders regard infestation as inevitable and therefore see no reason for complaining to their overseas suppliers. It has been difficult to persuade such traders, who often operate on very small margins, to recognize the need for fumigation or other treatment of infested goods. Recently, however, there has been an increasing resistance by processors and consumers to taking infested goods. This has been particularly marked in the case of large bakeries using imported flour and dried fruit, of sugar confectioners using edible nuts (walnuts, pea-nuts, almonds), of cereal breakfast food manufacturers using maize and rice, of canners using peas and beans, and, on occasion, even of animal feeding-stuffs manufacturers using groundnut cakes and rice bran.

Although these objections have been made primarily because of the mere presence of insects or insect damage, some have been because of storage risks.

Importing countries normally prefer, for reasons of economics, to thrust the responsibility for storage of the agricultural product on to the producer country and expect that country to send forward materials in good condition as required. However, if conditions of storage in exporting countries are poor, or certain types of goods are scarce, importing countries must keep stocks. These should be initially free from infestation and should be protected from cross-infestation from other infested imports. The latter risk may lead to rejection or diversion of imports. For example, an animal feeding-stuffs manufacturer declined to take into his port warehouse a cargo of infested wheat because he feared that it would contaminate other stocks. Users of commodities or traders holding stocks may find it necessary to have them fumigated or sprayed on arrival because the exporter cannot ensure their freedom from insects at time of shipment or during the voyage. For example, although Australian dried fruit is given injection fumigation at time of packing, all such fruit is re-fumigated on arrival in the United Kingdom, and is stored in specially selected warehouses, where it is regularly sprayed to prevent attack by indigenous pests.

Another aspect is the attitude of warehousekeepers, who may prescribe conditions of storage. Thus the Port of London Authority, having successfully reduced the resident population of *Ephestia elutella* in their tobacco warehouses to negligible proportions by routine insecticide spraying, has recently required the fumigation of all newly imported tobacco in which evidence of this species has been found.

FOOD HYGIENE: The attitude of the importer to infestation is considerably influenced by that of the public health officials responsible for the inspection of foodstuffs at time of

import and during distribution. Standards vary considerably from one country to another, but strict enforcement by countries with valuable markets can have a remarkable effect. Thus the activities of the F.D.A. of the United States (F.D.A., 1947), has not only protected the American consumer from eating infested foods, but has provoked the application of control measures in countries exporting to the U.S.A., with beneficial results to the internal markets of those countries and to other export markets. However, the fact that many countries have no proper import standards has meant that goods rejected by the U.S.A. authorities have been diverted elsewhere.

This emphasizes the need for a general raising of standards on the part of the principal importing countries.

**ECOLOGICAL ASPECTS:** It has been claimed, from time to time, that it is unnecessary to treat goods imported into temperate countries from those with warmer climates because the insects will fail to breed and will die during the winter. This argument fails to take account of various biological and commercial considerations. Thus some tropical pests are very cold-hardy at some stage of development, e.g. *Trogoderma granarium* (Solomon and Adamson, 1955), and others, susceptible to cold in unheated warehouses, may nevertheless survive in the centres of bulk or stacks of bags of grain or oilseeds. Heating due to the activity of the insects themselves can carry them through the winter. One cannot exclude the possibility that all or part of shipments of imported goods may be stored in heated premises. Imported flour stored during the war in heated cotton mills has shown development of infestation by *Tribolium castaneum* (Hbst.) and *Anagasta kühniella* (Zeller) in those parcels stored at a minimum of about 60°F, but not in those stored in unheated premises. Samples from bales or hogsheads of tobacco may be kept in heated rooms in tobacco factories. Under these conditions *Lasioderma serricorne* (F.) will breed, and when the sample is replaced insects will be reintroduced into the bale or hogshead, in which the original infestation has died out during winter storage. Under conditions of handling cargo in ports the receiver cannot be expected to distinguish between different species of insects, often almost identical, e.g. *Ephestia cautella* and *Ephestia elutella*, one of which can survive and the other not.

For these reasons, therefore, the tendency in the United Kingdom is to regard all infestations in imported produce as potentially dangerous and to permit climatic control only in special circumstances.

**APPLICATION OF PLANT QUARANTINE MEASURES TO STORAGE PESTS:** Regulatory control of the spread of storage pests by plant quarantine legislation is not generally favoured on the grounds that most storage pests are now established throughout the world in countries ecologically suitable for them and plant quarantine legislation is generally used to prevent or delay the spread of new pests rather than to control established species. It tends therefore to be used much more for the control of pests on material for propagation, seeds and fresh fruit and vegetables than for those which damage the plant product.

The International Plant Protection Convention (F.A.O., 1951) applies as clearly to storage pests of plant products as to those of plants in cultivation, and so does much national legislation. The following are examples of the current use of plant quarantine regulations against storage pests. Egypt requires cocoa beans and nutmegs to be free from *Areceus fasciculatus* (Deg.), otherwise entry is only permitted after heat treatment (Egypt, 1955); Chile requires fumigation, in ship before discharge, of grain found to be infested by *Sitotroga cerealella* (Chile, 1948); within the United States quarantine measures have been used since 1954 to try to stop the spread of *Trogoderma granarium* from California and adjacent states to the main wheat growing areas (Cotton, 1955). A strict quarantine against this species was established by Tanganyika and Kenya in 1956 (Tanganyika, 1956; Kenya, 1956).

In some instances the artificial division between plant products regarded as articles of commerce and those for propagation may frustrate plant quarantines, as when cottonseed for crushing for oil may be admitted without treatment, whereas cottonseed for planting must be fumigated. Importing countries should have the means to protect themselves against the introduction of infested stored products, whether by plant quarantine legislation, as in Canada, or by special stored products legislation as in

Great Britain, and by special technical inspectorates for this enforcement. By such means a country which is making a determined effort to reduce infestation by storage pests within its borders, can protect itself from reinfestation from without.

**TECHNICAL ASPECTS OF CONTROL:** The volume of infested commodities entering the principal consumer countries is so great as to make general treatment impossible. The policy, in Great Britain, is to try and ensure that a high proportion of valuable commodities, such as dried fruit and edible nuts is treated when necessary. For the remainder, treatment is recommended where the infestation is severe and where the commodity is likely to be distributed inland without processing. Fortunately much processing industry, of human and animal foodstuffs and of industrial raw materials is situated in the ports and the processing is generally adequate to kill insects. Provided the infestation is not so severe as to interfere with production or prevent safe storage of the commodity for the necessary period, treatment is not insisted upon. Control of transport after carriage of infested goods within a port or outside is essential to prevent cross and residual infestation and carriage of pests indirectly to places favourable for their breeding. The technical methods used for treatment are adapted, as far as possible, to the custom of the port, so as to cut down unnecessary handling. Thus fumigation in barges or under gas-proof sheets in transit sheds is preferred to removal to special fumigation chambers. Grain can be fumigated in port transit silos using chlorinated hydrocarbons. Such treatment would be much easier if port silos in the United Kingdom were equipped with circulatory fumigation plants as are many silos in ports on the European continent.

### GENERAL CONCLUSIONS

(1) *Infestation to be controlled before goods are exported.* It is clear that importing countries suffer losses and are put to a great deal of trouble in attempting to deal with infestations in imported goods. Much of this could be avoided if exporting countries controlled infestation before export.

There is today no excuse, on technical grounds, for the movement in international trade of badly infested commodities. Although proper facilities such as circulatory fumigation systems in elevators or fumigation chambers are desirable they are by no means essential, since fumigation of bulk grain is practicable in ordinary silo bins and of bagged goods in dock sheds under gas proof sheets.

(2) *Importers to be educated to demand pest-free goods.* What is needed is a greater demand, especially by the importers of commodities, that goods shall be uninfested on arrival. Competition between countries for markets for agricultural products has already caused certain exporting countries to lay down export quality standards and it is to be hoped that this tendency will spread. Pressure from importers is the most likely influence, and this will not occur until they realize that infestation is not inevitable.

In the education of the commercial community a considerable responsibility rests on the storage entomologist, particularly in major importing countries. Such educational activities should not be confined to traders and warehouse-keepers, but also extend to those concerned with the carriage of goods and the provision of ancillary services such as marine and cargo insurance. Once a favourable atmosphere of public opinion has been created, the application of regulatory measures, both in exporting and importing countries, is made much easier.

(3) *Storage entomologists in different countries to co-operate in research and application.* Cooperation between the storage entomologists of different countries is important especially in the exchange of information on the extent of infestation in products passing from one country to another. It is also important to see that those exporting countries whose technical services are poorly developed are provided with the necessary information to ensure that infestation can be controlled in their products. At the present time one might say that storage entomologists are distributed geographically in inverse proportion to their need. Since storage pests are cosmopolitan within their ecological limits, and the basic principles for their control are of universal application, they are particularly suitable for study on an international basis. More



should be done to co-ordinate the research and applied programmes of the different major centres, so as to avoid overlapping and to ensure the most economical direction of effort.

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I desire to acknowledge the assistance of my colleagues in the Infestation Control Division, especially the inspectors in the ports, on whose work in ships much of the main part of this paper is based. I would also wish to note that some of the information, especially relating to conditions in certain exporting countries was obtained during my period of secondment in 1954-55 to the European Productivity Agency of the Organisation for European Economic Co-operation.

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## DISCUSSION

J. D. BLETCHLY. As a representative of the Forest Products Research Laboratory, England, I would like to make two comments. First, failure to clean ships' holds thoroughly often results (in cases where mixed cargoes are involved) in the spread of *Tribolium* to timber in large numbers. The timber trade often mistake these insects for *Lyctus* and we are sometimes asked for advice after needless spray treatments have been carried out. Secondly, strict quarantine regulations may involve the exporting country in difficulties. For example, at present the Australian authorities are enforcing strict control measures against possible introduction of *Sirex* woodwasps as has occurred in New Zealand. This control involves inspection of softwood packing cases and on detection of exit holes the whole cargo may be condemned for fumigation by methyl bromide, thus raising the costs of the importer in a highly competitive market. Although this chiefly concerns the motor industry, it also involves all other industries using softwood in their packing cases. Inspection at the exporting end is difficult since detection of the tunnels is not easy in rough-sawn timber covered with sawdust and the employment of skilled staff for this purpose would increase the overhead costs.

H. M. ARMITAGE. Have you ever had occasion to reject imports of grain due to intolerant insecticide residues?

J. A. FREEMAN. Only once. A ship-load of wheat from Argentina had been treated at origin by the shipper using DDT with a six-inch layer of the dust applied over the load as a final precaution. This was considered sufficient reason by the Ministry of Food to prevent similar treatment of further shipments.

H. A. U. MONRO. In view of the fact that populations of moths have been observed in cargoes of Australian wheat entering the U. K., do the Australian authorities treat cargoes of grain prior to export?

J. A. FREEMAN. As far as I am aware there is normally no check of the infestation of Australian grain at the time of export. Exceptionally, importing countries which ask for weevil-free grain can have the grain inspected at time of export and obtain an official certificate. I do not know of any regular treatment at time of export. There is no system of inspection of ships.

E. J. GERBERG. Has the United Kingdom any regulations regarding tolerances of insecticides on imported grain?

J. A. FREEMAN. None.

# L'Entomologie des Produits entreposés au Portugal

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## ABSTRACT

*Jusqu'en l'année 1951, pratiquement aucune étude des insectes des produits entreposés n'avait été réalisée au Portugal. On ne connaissait alors, que quelques espèces dommageables contre lesquelles on appliquait les traitements en usage.*

*En 1951, les auteurs ont commencé à étudier le problème de l'arachide de la Guinée portugaise et, petit à petit, ils ont étendu ce plan de travail à d'autres produits de la Métropole et des Provinces d'Outre-Mer.*

*Grâce à l'aide de la "Junta" de Recherches d'Outre-mer et de la Direction Générale des Services Agricoles, ils ont pu poursuivre leurs recherches qu'ils ont divisées en trois sections: a) systématique, biologie, écologie et emmagasinage; b) moyens de lutte et biochimie; c) inspections entomologiques.*

*Il existe, actuellement, et pour la première fois, au Portugal, un groupe de techniciens agricoles et forestiers qui étudient ces problèmes. Ils constituent la "Brigade d'Etudes de Défense Phytosanitaire des Produits d'Outre-mer", du Ministère d'Outre-mer, et disposent d'un laboratoire servant à l'étude des produits d'Outre-mer. Conjointement, le "Laboratoire de Défense Phytosanitaire des Produits Entreposés", du Ministère de l'Economie, étudie les problèmes de la Métropole.*

*Dans leur communication les auteurs présentent aux membres du Congrès la situation actuelle de l'Entomologie des produits entreposés, au Portugal.*

On peut affirmer qu'avant l'année 1951, l'étude scientifique des insectes des produits entreposés a été presque nulle au Portugal, et la lutte aux plus nuisibles a été appliquée d'une façon tout-à-fait empirique. Il y eut des travaux antérieurs à cette époque, mais de par leur nature et leur nombre, ils ne présentent presque aucun intérêt. S'il est vrai que, sur ce point, le Portugal était en retard, on sait aussi que le dernier conflit international (1939-45), avec ses problèmes de stockage des denrées alimentaires et des produits industriels, a été le point de départ de telles recherches dans la plupart des pays.

Les premières tentatives d'études scientifiques de ces problèmes furent faites, entre 1942 et 1951, par Coutinho Saraiva et del Valle y March à la Répartition Technique d'Agriculture de Mozambique, par Aboim et Tordo à la "Junta" de Recherches d'Outre-mer, par Soromenho et Teles Grilo à la Station Agronomique Nationale, et par un des auteurs (C. M. Baeta Neves) à l'Institut Supérieur d'Agronomie. En 1951, des recherches exclusives sur ce sujet, furent organisées par un petit groupe dirigé par l'auteur déjà cité (C. M. Baeta Neves), au Jardin d'Outre-mer en collaboration avec la "Junta" de Recherches d'Outre-mer, du Ministère d'Outre-mer. L'année suivante (1952), ce groupe est transféré à l'Institut Supérieur d'Agronomie et, en 1954, il devient associé au Bureau des Services Phytopathologiques de la Direction Général des Services Agricoles du Ministère de l'Economie.

Depuis 1956, l'étude des insectes des produits entreposés au Portugal, s'accomplit à la "Brigade d'Etudes de Défense Phytosanitaires des Produits d'Outre-mer" du Ministère d'Outre-mer, et au "Laboratoire de Défense Phytosanitaire des Produits Entreposés" du Ministère de l'Economie, les deux sections étant sous la direction commune de l'un des auteurs (C. M. Baeta Neves).

Les recherches sont faites par des Ingénieurs Agronomes et des Ingénieurs des Eaux et Forêts, et se divisent en trois sections spécialisées: a) systématique, biologie, écologie et emmagasinage; b) moyens de lutte et biochimie; c) inspections entomologiques. Cette organisation est tout-à-fait transitoire.

Les travaux en cours ont pour but la protection des produits emmagasinés de la Métropole et des Provinces d'Outre-mer. Mais, à cause de la situation modeste de nos connaissances scientifiques, on a dû attacher d'abord un intérêt particulier aux études dites fondamentales.

Suivant cette orientation, on a fait le calcul des pertes causées par les insectes, champignons (moisissures) et bactéries, aux arachides de la Guinée portugaise, au coprah de S. Tomé et Mozambique, et à divers produits de la Métropole, pour obtenir une connaissance précise de leur importance économique. On a conclu que les problèmes d'Entomologie des produits entreposés au Portugal sont très sérieux.

Pour organiser la liste de la faune et de la flore qui les caractérisent, des inspections ont été faites dans les cargos, les magasins, les ports, chez les commerçants, dans les silos, les greniers et dans les usines de tabacs, amidons, pâtes, biscuits, farines de poisson, dans les minoteries, huileries, boulangeries et scieries de Lisbonne et ses environs, ainsi qu'en Algarve, à Madère, aux Açores, en Guinée, Angola, Mozambique, et aux Indes.

Pour bien connaître les conditions micro-climatiques des magasins, des études appropriées sont en cours, à Lisbonne, en Guinée et en Angola.

Après l'identification des espèces les plus importantes, nous en avons fait l'étude monographique (systématique, biologie et écologie). A date, les espèces étudiées sont les suivantes:

*Acanthoscelides obtectus* (Say), *Alphitobius ovatus* (Hbst.), *Alphitobius piceus* (Oliv.), *Anobium punctatum* (Deg.), *Calandra oryzae* (L.), *Carpophilus hemipterus* (L.), *Dermestes ater* Deg., *Dermestes maculatus* Deg., *Ephestia calidella* (Gn.), *Ephestia cautella* (Wlk.), *Ephestia elutella* (Hb.), *Ephestia kühniella* Zell., *Gnathocerus cornutus* (F.), *Hylotrupes bajulus* (L.), *Lasioderma serricorne* (F.), *Necrobia rufipes* (Deg.), *Nicobium castaneum hirtum* (Ill.), *Oligomerus ptilinoides* Woll., *Oryzaephilus mercator* (Fauv.), *Oryzaephilus surinamensis* (L.), *Pachymerus acaciae* Gyll., *Stegobium paniceum* (L.), *Tenebroides mauritanicus* (L.), *Thermobia domestica* (Pack.), *Tribolium castaneum* (Hbst.), *Tribolium confusum* J. du V.

Les procédés de détection des insectes, des acariens et de leurs débris dans les produits affectés ont également été étudiés avec soin. Déjà, quelques-uns sont employés dans les inspections, surtout pour le blé exotique importé par la Métropole.

Les moyens de lutte font l'objet d'essais de laboratoires et d'essais pratiques; jusqu'à présent, on a fait des recherches sur l'efficacité de différents produits insecticides (sulfure de carbone, bromure de méthyl, "Dowfume EB-5", "Dowfume EB-15", "Chlorasol", "Ventox", "Phostoxin", DDT, lindane, pyrethrines et pyrethrines + butoxyde de piperonil), ainsi que des recherches sur la technique des fumigations en chambre close, silos, dans des bateaux et sous bâches. Des méthodes d'analyse biologique et chimique de certains insecticides tels que le DDT et le lindane, et l'efficacité des appareils producteurs d'aérosols, ont également été étudiées.

Au cours de ces cinq années de travail, il nous a été possible de publier un grand nombre d'ouvrages sur les différents sujets de recherches et de faire connaître certains moyens pratiques de lutte contre la teigne des figues et les insectes de l'arachide emmagasinée, les deux problèmes les plus importants pour l'Algarve et la Guinée.

Pendant cette période, beaucoup d'élèves de l'Institut Supérieur d'Agronomie et des Ecoles de "Regentes" Agricoles ont fait leurs thèses à la Brigade ou au Laboratoire, apportant ainsi une collaboration précieuse.

Quoique l'organisation de la recherche dans l'Entomologie des produits entreposés au Portugal, soit loin de la perfection désirée, un groupe de spécialistes se consacrent exclusivement à l'étude de ces problèmes. Au cours de cette courte période (1951-56), on a acquis des possibilités d'obtenir, dans un avenir prochain, toutes les méthodes nécessaires de travail.

Le commerce et l'industrie commencent déjà à ressentir les résultats des études accomplies, et beaucoup d'entr'elles sont faites avec leur collaboration directe, dans le but de résoudre leurs problèmes pratiques les plus importants.



# The Stored Grain Insect Problem in Mexico.

## A Report of the Control Measures Now Under Study

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### ABSTRACT

*In 1952 it was estimated that about 15 percent of stored corn, wheat and beans were lost as a result of insect damage. The loss of these three basic food crops will become more serious with increased production and the consequent necessity of storage for longer periods of time.*

*Fifteen species of insects have been collected from stored grain. Of these, Sitophilus oryzae (L), S. granarius (L), Sitotroga cerealella (Oliv.), Ephestia kühniella (Zeller), and Plodia interpunctella (Hübner) are the most important in corn and wheat. In beans, Acanthocelides, obtectus (Say) in the central plateau, and Spermothrips pectoralis in the tropics are of greatest importance.*

*Results have shown that good commercial control of Sitophilus oryzae and S. granarius in seed corn and wheat can be obtained with DDT, methoxychlor and dieldrin, mixed with the grain at the rate of 50 p.p.m. The use of low concentrations of fumigants in grain destined for human consumption have given excellent results at Chapingo, Mexico. Carbon bisulfide and carbon tetrachloride mixed in the proportion of 1:4 and applied at the rate of 85 c.c. per cubic meter with a treatment period of 24 hours has given excellent control of S. oryzae in the laboratory and warehouses. Acrylon used at the rate of 70 c.c. per cubic meter, with a 24 hour exposure period has proved to be effective for the control of S. oryzae.*

Problems in the storage of corn, wheat and beans are more frequent and severe in Mexico at the present time than they were in the past. They will become more frequent and more severe in the future. The basic reasons for this are two: First, there is now a greater production of the basic food crops and therefore, greater quantities of grain are going into long term storage in official, semi-official and private warehouses. Secondly, the harvests which result from the increased agricultural development in the tropical regions of Mexico must be warehoused under tropical climatic conditions for indefinite periods of time before the excess can be shipped to the centers of consumption. During this time the grain is exposed to insect infestations which later develop to alarming proportions, before the grain is finally distributed to the ultimate consumer.

The production of wheat has trebled in the past five years, increasing from approximately 400,000 tons in 1950 to 1,200,000 tons in the crop year 1955-1956. This increased production is the result of many factors, but the most striking one is the opening of new areas of production, as for example in the states of Sonora and Sinaloa. This year the state of Sonora alone produced as much wheat, approximately 450,000 tons, as did all Mexico in 1944. A similar story can be told for corn. Corn is produced more generally in Mexico than wheat, and production has climbed steadily since 1940. It is estimated that about five million tons of corn will be produced in 1956.

According to the "Boletín Mensual de la Dirección General de Economía Rural", for 1954, Mexico was importing approximately 46,000 tons of beans annually. Essentially the same situation exists at the present time. Because of the underproduction, beans are rapidly consumed, thereby reducing the storage problem. Supply will continue to be short for some time and therefore storage problems are not as apparent with this commodity as they are with corn and wheat. Wherever beans are stored, however, there is a serious problem of insect infestation.

To my knowledge there has been no accurate determination of the losses of stored grain in Mexico. I think that the average losses which have been reported as varying from 15% to 25% are probably high. There is no doubt, however, that great losses of stored grain are sustained every year. Let us assume for a moment that an average of only 5 percent of the 1954 corn crop, which was about 4.5 million tons was lost or made unfit for human consumption. This is equivalent to about 225,000 tons. The official price for corn was the equivalent of about \$44.00 (United States currency)

per ton; therefore the monetary loss would be about the equivalent of \$10,000,000.00 United States dollars. This quantity of grain or amount of money can be ill afforded by Mexico.

General estimates of losses sustained by some of the Latin American countries are given in Table I (Parkin, 1956). The data presented here for Mexico were not obtained from this report but are based upon other published estimates.

TABLE I—Estimated Losses of Corn, Rice and Pulses during the Period from 1947-49. United Nations. Data taken from Annual Review of Entomology. Vol (1): Estimates for the first seven countries obtained from a Working Party of 224-225. 1956.

El Salvador	25%
Guatemala	25
Honduras	50
Nicaragua	30
Costa Rica	45
Haiti	47
Uruguay	14
Mexico*	15-25

\*Other reports.

Surveys have shown that about twenty species of insects may be found in stored grain and warehouses in Mexico. However, of this group the weevils, *S. oryzae* and *S. granarius* are the most important in corn and wheat. In beans *Acanthoscelides obtectus* is the most troublesome in the high central part of Mexico and *Spermophagus pectoralis* is responsible for the damage in the tropics. The moths, *Ephestia kühniella*, *Plodia interpunctella* and *Sitotroga cerealella* make up the second insect group of importance in stored corn. The remaining fifteen species are of lesser importance but under special circumstances they have been responsible for severe damage and losses in grain.

The stored grain insect control investigations being conducted in Mexico may be divided into two general fields. First, studies of the control of insects in the large warehouses of privately owned mills and of the official and semi-official agencies of the Government, such as the two credit banks. In addition to these governmental agencies which warehouse and distribute grain for human consumption there are also other official agencies such as the National Corn Commission which store and distribute improved seed of one or all of the basic food crops. The second field of investigation is farm storage, where the protection of smaller quantities of grain, both for seed and for home consumption, is of greatest importance.

I will now briefly discuss what has been done and the results obtained in each of the two fields of study.

**INSECT CONTROL IN LARGE WAREHOUSES:** Modern large capacity warehouses are being constructed for storing large quantities of grain, to replace the old inadequate structures now in use. The greatest proportion of grain stored in these warehouses is destined for human consumption and therefore only fumigants are used for insect control. The reason that greater losses do not occur is that the stocks are rapidly consumed and do not remain in supply depots for sufficient time to permit insects to cause excessive damage. The fumigants most commonly used are methyl bromide applied at dosages varying from 1 to 3 pounds per thousand cubic feet for exposure periods of from 8 to 24 hours. Calcium cyanide mixed with the grain as it is put in the silos has been used rather extensively.

Tests made by the Oficina de Estudios Especiales, of the Secretaria de Agricultura y Ganaderia have shown that either Acrylon, or a preparation of carbon bisulfide and carbon tetrachloride mixed in the proportion of 1:4 has given good commercial insect control in corn and wheat; with no deleterious effects on the germination. Dosages of 85 cubic centimeters per cubic meter of the carbon bisulfide, carbon tetrachloride

mixture, and 70 cubic centimeters per cubic meter of acrylon are being recommended. Methyl bromide used at the rate of one pound per thousand cubic feet has also proved satisfactory for insect control in seed corn.

Methyl bromide has been suspected of damaging the germination of seed corn. Concentrations as high as 3 pounds per thousand cubic feet and the exposure periods of as much as fifty-two hours were used in some seed corn. Temperatures inside the building during the fumigation reached 41°C.

Hydrocyanic acid applied at the rate of 1.5 pounds per thousand cubic feet is also being used, in one seed warehouse. This warehouse is still under study and the results with respect to insect control are as yet incomplete.

Only fair to good control has been obtained with the use of fumigants. I think the two principal reasons for these results are: (1) rapid reinfestation following fumigations and (2) because of the inadequate building construction it is very difficult to maintain a sufficiently great concentration of gas to assure proper penetration and, therefore, good control. Since much of the grain is handled in bags the use of spot fumigation holds a promising future. This method of fumigation is rapid, readily adaptable, and manageable in the large reconditioned structures which have been converted into warehouses.

We find that at altitudes of about 2000 meters or above, lower concentrations of acrylon and the mixture of carbon bisulfide and carbon tetrachloride are needed to give excellent insect control than are generally recommended for these fumigants when used at lower altitudes. It is recommended in the United States that 1.5 gallons of the carbon bisulfide carbon tetrachloride mixture per thousand bushels of grain be used. This is the equivalent of 5.6 liters of the mixture per 32.7 cubic meters. It has been found that good commercial kills can be obtained with only 3 liters per 36 cubic meters. The same situation holds true with acrylon treatments. We in Mexico do not understand why this difference in concentrations should exist. Is it because of lower atmospheric pressure at the high altitudes which permits more rapid volatilization? Further more detailed investigations are planned to determine why good commercial control is obtained with these low concentrations of fumigants at high altitudes.

In the large warehouses very few preventive measures for insect control are practiced. Driers are now being used more extensively and the use of residual treatments of insecticides in the warehouses before grain is stored in them is becoming a more common practice. We are recommending that sprays of DDT 2.5% by weight be used to treat the interior of the storage places. Equally as good results have been obtained with lindane, chlordane and dieldrin sprays, but since DDT is the most readily available it is being recommended at the present time.

**THE PROTECTION OF GRAIN STORED ON THE FARM:** The use of fumigants on farms for the present is out of the question, as the farm storage facilities in most cases do not permit the use of gases for insect control. Their use is made even more impossible when the grain is stored in dwellings, a common practice on many farms. The use of insecticides mixed with grain to function as protectants is not practical, because the corn, wheat or beans will, in all probability, be sold or eaten before they can be planted the following crop season. The use of materials such as pyrenone cannot be recommended as they are much too expensive and the residual effect is too short, especially in the tropics. Insect control on the farm at the present time is restricted to the treatment of a properly conditioned storage area with residual insecticides, and a strict clean-up of the granaries to remove all old grain which serves as points of reinfestation. On farms the corn, wheat and beans are left standing in the fields to sun dry before harvest. In addition to this, practically all farms have a drying area in which the food crops are spread out for further exposure to the sun before they are put in the warehouse. Table II shows how the moisture content of dried grain varies during one year's storage in the high central part of Mexico as represented by Chapingo, and in the tropics as represented by San Rafael, Veracruz. In central Mexico very little change occurs in the moisture content of grain even during the wet season from June to September. In the tropics, however, there is a definite increase in the moisture content of the grain during the wet season. Under the high temperature conditions grain of 15 to 17 percent moisture soon becomes severely damaged with insects and molds.



If there is assurance that the grain is to be used as seed alone it has been found that DDT used at the rate of 50 p.p.m. of grain gives excellent protection for at least 8 months. Dieldrin, chlordane, BHC and toxaphene have also been found effective, but since DDT is most readily obtained this material is recommended for the present.

TABLE II—Moisture Contents of Corn and Wheat Stored in Bags at Chapingo and Corn at San Rafael, Veracruz. Samples Taken at Monthly Intervals.

	Wheat	Chapingo Corn	San Rafael Corn
January 1955	10.5%	9.2%	—
February	9.6	8.7	—
March	10.1	9.5	—
April	9.8	10.0	9.0%
May	10.2	10.2	9.5
June	10.8	10.1	10.5
July	10.7	10.4	10.7
August	11.8	11.0	14.0
September	12.6	12.2	14.3
October	12.5	13.4	17.1
November	12.3	12.0	15.5
December	11.4	10.6	15.0
January 1956	11.0	8.8	14.7

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Parkin, E. A. 1956. Stored product entomology (The assessment and reduction of losses caused by insects to stored food stuffs). *Annual Review of Entomology* I: 223-240.

#### DISCUSSION

M. H. BREESE. Referring to your remark that temperatures in a warehouse during a fumigation reached 41°C., this is only 1°C. below lethal temperature for most stored product insects. Have efforts been made to store grain in large tight stacks of bags and thereby achieve heat "self-sterilization" of grain?

D. BARNES. No, but experiments are contemplated. Many farmers in the tropics store their grain in steel drums and leave them exposed to the sun. Inspection has shown that the grain under these conditions is free of insect attack.

L. M. REDLINGER. What was the temperature of the grain at time of fumigation?

D. BARNES. 18 to 20°C.

E. A. PARKIN. Is there a tolerance limit in Mexico which prevents the admixture of 1 p.p.m. lindane to corn to prevent attack by the rice weevil?

D. BARNES. No. There are no tolerance limits for insecticides in stored products there.

H. A. U. MONRO. At high altitudes the need for lower doses of fumigants might be partially explained by their more rapid evaporation and speedier penetration brought about by prevailing lower atmospheric pressures (circa 580 mm.) tantamount to a fumigation under partial vacuum.

H. M. ARMITAGE. Regarding the effect of methyl bromide fumigation on seed germination, the California State Seed Laboratories, cooperating in the measures directed toward eradication of the Khapra beetle have found that exposure of leguminous seeds to 5 lbs. methyl bromide per 1,000 cu. ft. for 48 hours does no significant damage to germination if the moisture content of the seed is less than 10 per cent. Cereals have been equally tolerant. Oil-bearing seeds as cotton seed, etc., show some damage on first exposure but it is not truly significant. However, a second exposure of the same seed to the same treatment causes serious germination damage.

# A Theoretical Evaluation of the Potential Range and Importance of *Trogoderma granarium* Everts in North America (Col. Dermestidae)<sup>1</sup>

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## ABSTRACT

The intrinsic rate of increase of many stored products insects can be calculated for constant conditions from the developmental period, mortality, sex ratio and oviposition performance. This may be taken as the maximum rate of increase possible in the given conditions. A graph has been constructed for *Trogoderma granarium* Everts fed on malted barley showing how temperature and humidity affect the rate of increase. Superposing climatographs for various places in the world on to this graph shows quickly whether or not this species is likely to be a pest in those places. Rough estimates are made of the potential annual increase in a few places. It is suggested that *Sitophilus* spp. and *Rhyzopertha dominica* are likely to restrict *Trogoderma granarium* as a pest to the hotter drier places, but the heating caused by these beetles may produce an environment unsuitable for themselves but suitable for *Trogoderma*. It is thus possible to predict the limits of distribution of this species by considering climate, the artificial heating of premises and the natural heating of produce and to estimate its probable economic importance. The predictions are somewhat limited by lack of data on warehouse conditions and by a tendency for *Trogoderma granarium* larvae to enter a resting state in conditions quite suitable for normal growth. This reduces the rate of increase but enables the larva to withstand starvation, low temperature and many control operations.

It is comparatively easy to breed most stored produce pests in the laboratory in constant conditions. It is convenient, therefore, to study their life cycles and obtain data at constant temperature, constant relative humidity at a fixed density (often 1 per tube) on a measured quantity of a standard food. Their oviposition rates can be found in similar conditions. From such data for developmental speed, mortality, sex ratio and oviposition performance, a statistic can be calculated, the intrinsic rate of increase, which can be taken as the maximum rate of increase for the species in the given conditions when a stable age distribution is reached. It is possible to cover the entire temperature and humidity range of a species at constant conditions; we have at the Pest Infestation Laboratory, for instance, eleven temperatures available simultaneously and five or more relative humidities can be used at each. Given data for combinations of constant conditions it is possible to predict with a fair degree of confidence the effects of variable conditions which occur naturally, at least where the variations do not reach extremes of cold or dryness or much exceed the optimum. The validity of a few predictions of this kind has been tested for certain controlled variations obtained in a special incubator.

In the present paper, some conclusions are drawn for the Dermestid, *Trogoderma granarium* Everts. This seems a useful approach to this species which is extremely difficult to detect at low density and gives the impression of increasing explosively at times. Before 1939 it was a pest only in Asia (India, Pakistan, Persia, Iraq), Africa (Egypt and the Sudan) and in certain specialised environments in maltings in Europe. In recent years it has gained entry into and been found in Nigeria, French Niger and possibly other parts of West Africa, Nyasaland, the Rhodesias and South Africa as well as the U.S.A.

The published data which form the basis of this paper (Hadaway, 1956) were obtained at the Imperial College in 1938-9 by Dr. Hadaway, who used five temperatures and four relative humidities at each with malted barley for food. His data on developmental speed, mortality, sex ratio and oviposition rate have been used to calculate the intrinsic rate of increase. From the values for the 14 conditions at which

<sup>1</sup>This subject is considered further by R. W. Howe and D. L. Lindgren in *J. econ. Ent.* 50: 374-375. 1957.

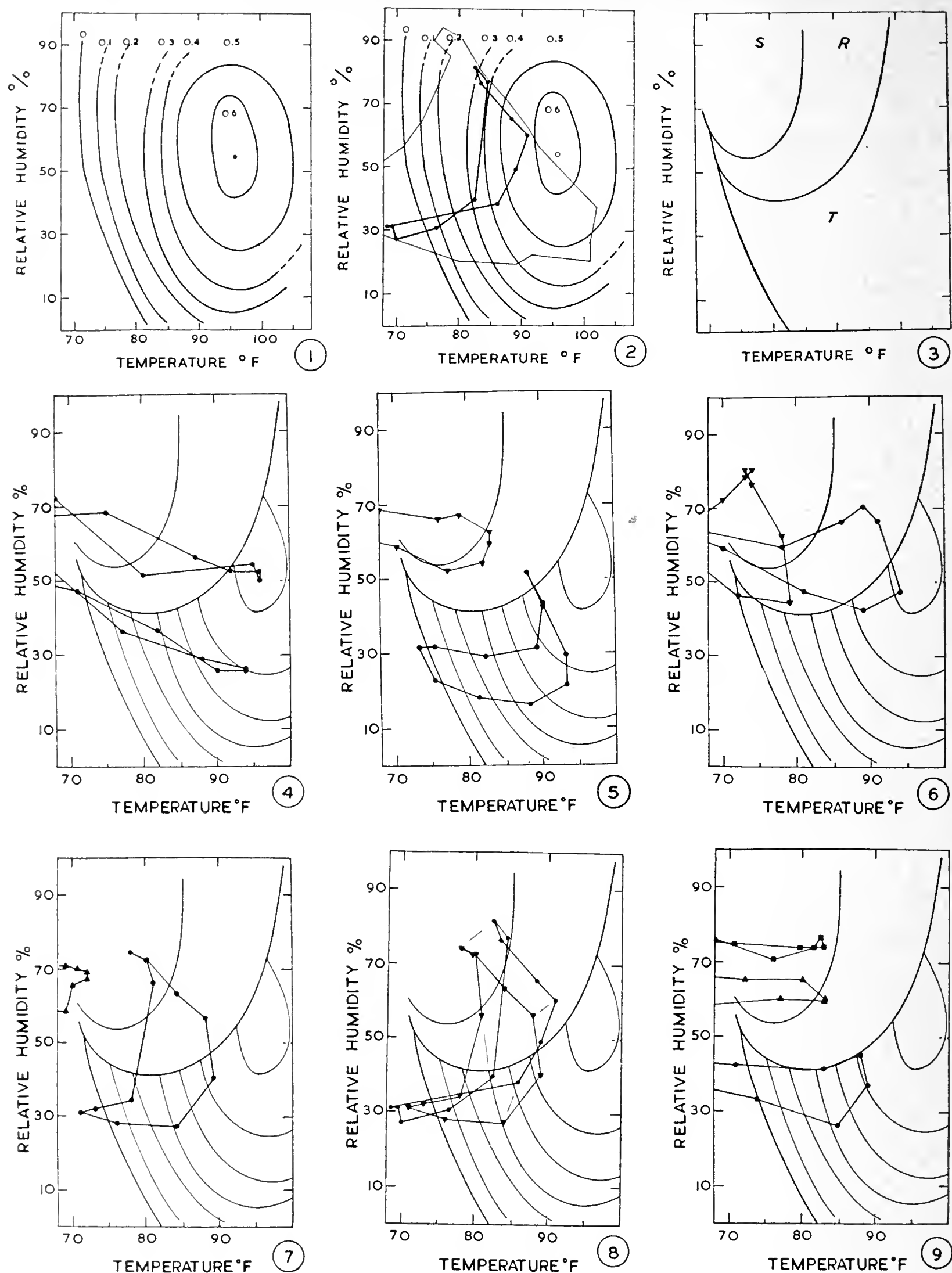


Fig. 1. The intrinsic rate of increase of *Trogoderma granarium* at various combinations of temperature and humidity as calculated from the data of Hadaway (1956).

Fig. 2. Climatographs for mean and extreme conditions in a Kano warehouse superimposed on data for rate of increase of *Trogoderma granarium*.

Fig. 3. The temperature humidity zones which favour *Sitophilus oryzae* (S), *Rhyzopertha dominica* (R), and *Trogoderma granarium* (T).

Figs. 4-9. Climatographs superimposed on Fig. 3 to show likely importance of *Trogoderma granarium*. Fig. 4, Basra (above), Hinaidi (Baghdad). Fig. 5, Cairo (▲), Khartoum (●), Fig. 6. Broken Hill (▲), Lahore (●), Fig. 7. Pretoria (▲), Kano (●) Fig. 8. Kano (▲), Kano warehouse (●). Fig. 9. New Orleans (■), Fort Worth (▲), Phoenix (●).

development was possible, lines have been drawn, (Fig. 1) smoothing out the experimental variations, to show the conditions in which the value of this statistic is 0.1, 0.2 up to 0.6. The weekly self multiplicative rate corresponding to these values and to the highest value obtained are shown in Table I.

TABLE I—Self Multiplicative Rates of Increase Corresponding to Given Values of the Intrinsic Rate of Increase ‘r’.

‘r’	Percentage increase per week
0.1	10
0.2	22
0.3	35
0.4	49
0.5	65
0.6	82
0.64	90

If the environmental conditions in a warehouse or a stack of produce are plotted on a similar scale and superposed on Fig. 1, it is immediately obvious if the conditions are suitable for the insect. A Kano warehouse (Fig. 2) does suit *T. granarium*. Unfortunately little data of this kind is available to us and that which we have is for British warehouse conditions. These are outside the range of *T. granarium*. Consequently it is necessary to rely on standard meteorological data, bearing in mind its limitations. For simplicity, mean temperature and mean relative humidity for each month may be used. These may be plotted as climatographs as in Fig. 2 and the corresponding values of r (per month) may be added to give an estimate of the maximum annual increase of *Trogoderma granarium*. Table II gives the annual increase so calculated for places

TABLE II—Maximum Annual Increase of *Trogoderma granarium* Estimated from Standard Meteorological Data.

Asia - Africa		U.S.A.	
Khartoum	10 million	Key West	2,500
Basra	2 million	Phoenix	1,250
Abadan	11½ million	San Antonio	625
Jodhpur	1 million	Fort Worth	525
Lahore	1 million	New Orleans	475
Kano	350,000	Montgomery	200
Cairo	1,600	Charleston	110
Broken Hill	32	Memphis	50

in a number of Asian and African countries in which the species has been found, and the potential values for a similar number of places in the U.S.A. Many of the values are so large as to be meaningless except to show the magnitude of the control problem, and cannot be realised because of crowding effects, food shortage and so on. A value of 500 is certainly of pest proportions and values of 100-200 would probably be also.

The problem cannot, however, be considered without some reference to other species which in some ways encourage *Trogoderma* and in other ways discourage it. The encouragement is principally the initiation of heating by other species which is frequent in temperate countries and very common in tropical ones. Among grain insects, for instance, both *Sitophilus oryzae* (L.) and *Rhyzopertha dominica* F. can cause heating up to 42°C. although their upper breeding limits are about 34° and 38°C. respectively. These and other species can start the process in produce which is too cool for the breeding of *Trogoderma granarium* and eventually render much of it too hot for themselves but ideal for *T. granarium*. It is not unusual to find a bulk of grain with weevils at the surface and *R. dominica* in the sub-surface layer. Deeper in such a bulk the temperatures would be suitable for *T. granarium* the presence of which may be

completely unsuspected from the outside. Heating, of course, rules out the use of climatographs, and often effectively eliminates the influence of the cool season.

The adverse effects of other species arise from some form of competition. The works of Birch, Crombie, Park and others have shown that in laboratory cultures, it is not possible to breed indefinitely more than one species in a culture unless the species occupy very different niches. This seems broadly to be true in warehouses also, except that the variety of niches and their size is larger so that the final members of the subordinate species survive much longer. Generally speaking the surviving species is that with the higher rate of increase but exceptions must obviously occur when one species influences the rate of increase of another, by predation for instance or by making the food more easily available.

Making this assumption that the species survives which has the higher rate of increase, ignoring the effects of initial density, and using the data given by Birch (1953) for *S. oryzae* and *R. dominica* and that given earlier in Fig. 1 for *T. granarium*, it is possible to delineate the areas of environmental conditions in which each of the three species is the most favoured (Fig. 3). Thus the cooler damper environment suits weevils, a warmer drier environment suits *R. dominica*, and the hottest, driest environment is left to *T. granarium*. A similar division could be made between *Tribolium castaneum* and *T. granarium* for groundnut storage. The importance of *T. granarium* is therefore reduced by the pressure of these other species in the more humid environments and its importance is greatest in dry regions such as Hinaidi (Iraq) and Khartoum (Figs. 4 & 5). It will be seen from Fig. 5 that Cairo lies entirely in the weevil-*R. dominica* zones. It is probable that moving south from Cairo to Khartoum, *Sitophilus oryzae* would give way in dominance to *R. dominica* and then to *T. granarium*. Figures quoted by Zacher (1935) give some support to this idea (Table III) for they show a clear change in dominance between *Sitophilus* spp. in the Nile delta and *T. granarium* at Luxor. His records of *T. granarium* are partly due to heating and partly to recent import from the south. The importance of *T. granarium* in Iraq (Fig. 4), Pakistan & Northern Rhodesia, (Fig. 6), Nigeria and South Africa (Fig. 7) is partly due to heating of buildings (Fig. 8) or of produce—in South Africa and Southern Rhodesia, it must be almost entirely due to this cause.

TABLE III—Percentages of Grain Samples (etc.) Collected by F. Zacher (1935) in Egypt in March - May Found Infested by Three Species.

Place	<i>Sitophilus</i> spp.	<i>Rhyzopertha</i> <i>dominica</i>	<i>Trogoderma</i> <i>granarium</i>
Alexandria	94	71	0
Benha	100	43	0
Cairo	100	38	17
Rod el Farog (Cairo)	91	46	18
Atr en Nabi	70	30	60
Luxor	40	0	80

In the U.S.A., Phoenix, Arizona, (Fig. 9) has the type of climate which suits *T. granarium* but not the other species, but the high humidity of New Orleans and Key West favour the weevils. Maps (Nos. 155-6, 265-6) given by Visher (1954) which show the periods for which mean and maximum temperatures exceed 75°F. mark off fairly well those areas of the U.S.A. which are open to invasion by *T. granarium*. Heating of produce and of buildings extends the area of risk unpredictably, and could lead to an occasional outbreak in the more humid eastern area. In the main, however, the area of importance for *Trogoderma granarium* should be restricted to the arid south west and Mexico. Fig. 10 shows that Australia, and South America may also be open to invasion by the species.

Two final points should perhaps, be mentioned. Harmful low temperatures appear to be well below the developmental minimum, so that an appreciable amount of growth may occur when the mean temperature of a varying environment is too low for



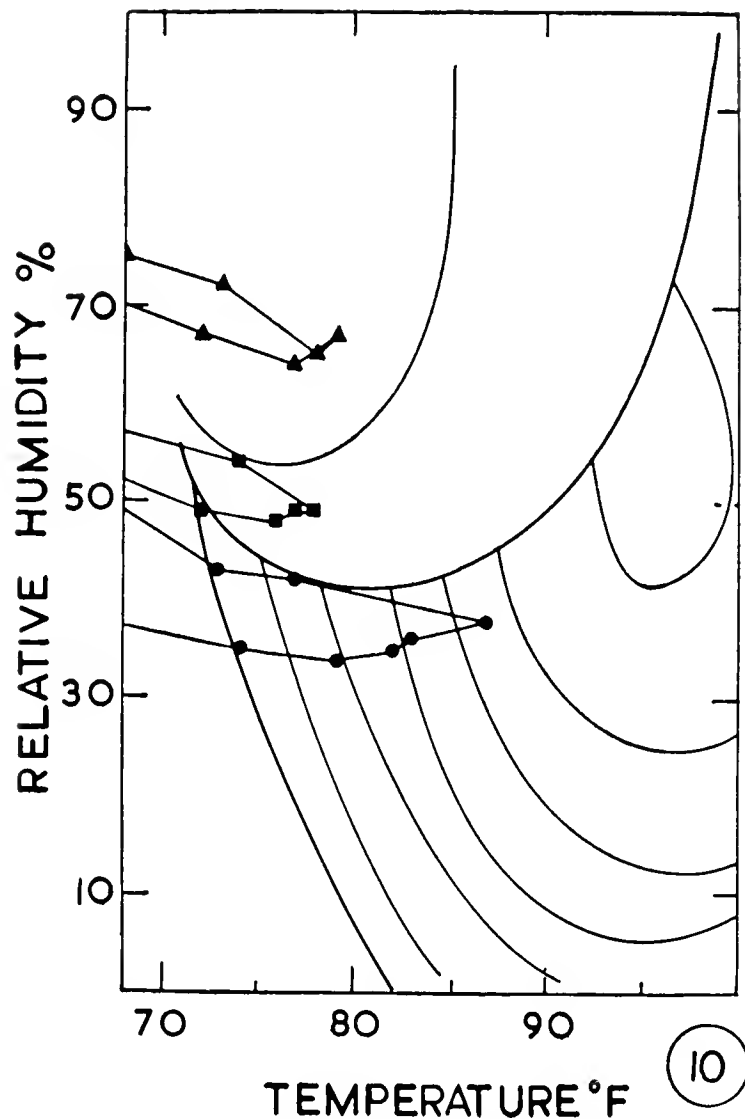


Fig. 10. Climatograph of Parana (▲), Port Augusta (■), and Alice Springs (●) superimposed on Fig. 3 to show likely importance of *Trogoderma granarium*.

development. This probably is not important for Burges has shown (in unpublished work) that the larvae of this species readily enters a resting stage especially at temperatures below 85°F. in several slightly unfavourable conditions. This stage is usually passed in a crevice and helps the larvae to survive long periods of starvation, low temperature and insecticidal sprays.

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### DISCUSSION

A. SHULOV. The eggs of *Trogoderma* develop under conditions of 0% relative humidity. The meteorological climatographs are inapplicable for *Trogoderma* because the conditions in a grain heap are completely different. The larvae are able to remain for years in a resting stage. Attention must therefore be turned to perfect cleaning of the barns.

R. W. HOWE. Yes, this paper is based on the work of Hadaway who used phosphorus pentoxide to give a relative humidity of about 3%. The climatographs using meteorological data are of course inapplicable when heating occurs. What is necessary is a measure of the real environment.

H. A. U. MONRO. Does the resting stage of *Trogoderma* larvae demonstrate decreased respiration? Work by Bond at the London (Ont.) Laboratory (now in press, *Can. Jour. Zool.*) has shown that the susceptibility of some insects to methyl bromide fumigation is directly related to their rate of respiration.

R. W. HOWE. Yes, in the resting stage the respiration rate is extremely low. The larva in this stage, hiding in a crevice, is extremely resistant to methyl bromide fumigation.

H. M. ARMITAGE. Have you determined the minimum lethal temperature and humidity to all stages of *T. granarium*? Also can larvae remain out-of-doors as individuals at winter temperatures about 26°F. rising during daytime to 60°F.?

R. W. HOWE. *Trogoderma* can withstand "zero" humidities and still grow. We have not determined its minimum temperature tolerance but we know it can withstand the British winter. I would expect it to withstand 26°F. for some time.



# Grain Sanitation on Kansas Farms<sup>1</sup>

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## ABSTRACT

Six years of observations of the effects of various management practices employed by approximately 335 Kansas farmers on infestations of grain damaging insects in market grains are reported. Important management practices included: 1. Good house-keeping procedures; 2. Separation of market grain from animal feed and seeds; 3. Storage in granaries isolated from animal shelters and haybarns.

An intensive survey of 115 farms indicated that accumulations of grain large enough to support populations of grain-infesting insects were present in various farm buildings. Approximately 17 per cent of garages, 45 per cent machine sheds, 50 per cent haymows and 84 per cent of mangers had such accumulations. The most abundant insects in farm buildings outside of the granary during July and August were *Oryzaephilus surinamensis* and *Laemophloeus* spp. Feed rooms had more than 15 grain-damaging species. Of various sites examined, 9 species were collected from truck beds, 8 from hay mows, 11 from feed grinding equipment, and 12 from mangers.

However insect sanitation in farm granaries did not result entirely from accumulations of litter and spilled grain. Many tidy and apparently clean granaries were found to be infested, particularly when newly harvested grain was binned close to feed grains and ground feeds. Also market grains stored in animal shelters where heat, moisture and feeds favored insect development or in hay barns which provided shelter, seeds and nutritious dusts were likewise unsanitary.

Removing the causes and eliminating the sources of infestation by proper management practices provide the first and least expensive control measures in a grain sanitation program. Important management practices include: 1, granary cleanup; 2, separation of market grains from animal feed and seeds; and 3, storage in granaries isolated from animal shelters and haybarns. Insecticides are only adjuncts to these more fundamental control measures.

Extensive investigations of granary sanitation and management practices were made on 335 Kansas farms during a six-year period beginning in 1950. These included an intensive survey of 115 farms to determine which farm practices affected the quality of the wheat in storage (Wilbur and Warren, 1953, 1954). Some attention was paid the granary but more was given to farm activities and buildings other than those concerned directly with grain storage. The objective was to determine what relationship such enterprises as poultry, hog, cattle, hay, and seed production might have to infestation of stored grain by insects.

**CONDITIONS IN FARM BUILDINGS (OTHER THAN GRANARIES):** All buildings including barns, poultry and hog houses, animal sheds, machine sheds, tool sheds, and garages were inspected. All grain and feed residues that provided enough food to support grain-infesting insects were recorded.

Grain or feed residues were found in all types of buildings. Seventeen percent of the garages and 22 percent of the tool sheds examined had such residues. Of 121 mangers in barns, 84 percent had feed accumulations. Of 126 sites examined in runways, alleys, and driveways in barns, 83 percent had accumulations of grain. Approximately half of the hay mows and hog houses contained grain, seeds, or feed.

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INSECTS IN ACCUMULATIONS IN FARM BUILDINGS: At least 15 different species of grain-infesting insects were found in farm buildings other than granaries. *Oryzaephilus* was collected from the most sites, followed by *Laemophloeus*, *Plodia*, and Dermestidae. All 15 species were taken in feed rooms and in barreled or sacked grain stored in the various buildings. Poultry houses yielded 13 species; mangers, feed boxes, and corn cribs had 12 species; even hay mows had six species of which *Oryzaephilus* and dermestids were in greatest abundance.

INSECTS IN FARM MACHINERY AND EQUIPMENT: Nine insect species were found in truck and wagon beds frequently parked in granary driveways. In many trucks, infested grain or feed had been left in the beds; in some the beds were clean but insects lived in cracks or between the floors. Such evidence points to vehicles, which transport feed and grain, as important means for spreading insect contamination. Insects also were found in feed grinders and hammer mills, and in elevator pits, combine hoppers, and seed drills.

ACCUMULATIONS IN OR ABOUT FEED ROOMS OR BINS: Waste grain and feed residues were scattered overhead, in the walls, on the floor, under floors, and outside the doors of 90 percent of the feed rooms examined. Grain and feed dust had accumulated on overhead sills and cross members, on overhead floors, occasionally on the under surface of the roof and on all structures that provided lodging places. Also, broken kernels and dust were in cracks, tunnels in wood formed by cadelle beetles, and on spider webs on the walls of bins. Spilled grain and feed were just outside of 47 percent of doorways and underneath 44 percent of the floors.

The same species were in feed rooms as in farm buildings and in essentially the same order of abundance.

ACCUMULATIONS AND INFESTATIONS IN GRANARIES OR GRAIN BINS: A search for accumulations of waste grain was made at 2,339 sites in 108 buildings in which grain was being stored, and in 702 bins. As in the feed rooms, such accumulations were in every part of the bins and granaries from overhead projections to the floors and under the floors. Most were in granary driveways, on bin floors, and in corncribs. Spilled grain occurred in nearly half of the bin doorways, on the outside sills, and on the ground or floors below the sills. Also, accumulations of dust or grain were above the bins and clinging to bin walls.

It is obvious that granary cleanup is an important management practice. However, many infestations in market wheat did not start in littered grain or feed. Tidy and apparently clean granaries also were infested, particularly when newly harvested grain was binned close to feed grains and ground feeds. Thus, *separation of market grain from feed grains, ground feeds, and seeds* is also an important management practice.

Market wheat is held in farm storage in Kansas for only a short time; much of it is moved into commercial channels within six months following harvest, and most of it within nine months. Feed grains and ground feeds may be held for long, indefinite storage.

There is a close relationship between extent of infestations and length of storage. Isely (1947) found that continuous storage was one of three factors that determined the extent of weevil infestations in corn in Arkansas. A survey conducted in Denmark by Wichmand and Borlund (1953) revealed that infestations were more prevalent in grain on farms of rich farmers than on farms operated by farmers of more limited means. Rich farmers held their grain longer and thus provided greater opportunity for infestations.

In Kansas, *Tenebroides*, *Laemophloeus*, *Oryzaephilus*, and *Plodia* infest wheat shortly after harvest and with favorable conditions develop into a population peak by September. Rice and granary weevils and lesser grain borers seldom are found in market wheat before late summer and then in small numbers, though they may be found in large numbers much earlier in feed grains.

Approximately 62 percent of the farms on which market wheat was stored also had feed grains and ground feeds in bins adjacent to the market wheat. Spillage was common and trails of feed were found all along driveways. On occasions, grinders were

installed in a large storage bin or in the driveway. Feed grinding results in the horizontal granary surfaces and the walls becoming heavily coated with a dust that is highly nutritious for grain-infesting insects. Also, the grinding machinery is so heavy and cumbersome that it is seldom moved and spilled grain and feed become deeply lodged about it. Feed rooms are particularly difficult to clean and to maintain clean and are difficult to spray or fumigate.

Feeding commercially milled feeds is an ever-growing practice among Kansas farmers. The milled feeds frequently are stored in the bins, stacked along the driveway, or piled on top of market wheat. The quality and balanced nutrients that make these feeds valuable for livestock and poultry also make them desirable for grain-infesting insects. During July and August most commercial feeds on the farms were infested. Seeds constitute the same problems as feeds if they are retained for long periods.

No matter what efforts are made by farmers to destroy infestations in their market wheat, when feeds or seeds are stored close by, reinfestations are inevitable. Storing feeds and seeds adjacent to market wheat should be avoided whenever possible. When this is not practical, the feed grains should be fumigated when the bins to receive the newly harvested wheat are cleaned and sprayed. This should prevent further damage to the feed and prevent insect migration to the new wheat.

**AVOIDING ANIMAL BARNs FOR STORING MARKET WHEAT:** Insect populations in wheat in Central Kansas normally reach their peak by mid-September and then drop off sharply with the cooler fall temperatures so that by mid-November the numbers are low. Few grain-infesting insects can hibernate. Most insects in grain stored in isolated granaries do not survive the cold of ordinary Kansas winters so that many Kansas granaries are effectively sterilized of grain-damaging insects each winter.

Twenty percent of all of the grain storage bins surveyed in Central Kansas were located in buildings that housed animals, generally cattle. The heat and moisture provided by the animals and their manure create a highly favorable environment for insects. As a result the normal winterkill is reduced substantially or does not occur at all. Isely's (1947) investigations in Arkansas showed that 43 percent of the corn cribs in barns were weevil-infested as compared with 13 percent infestation of cribs separated from barns.

Mows or stacks of hay and straw, usually found in animal barns, also help to stabilize the warm temperature of the grain and to prevent its cooling with the onset of winter. When stored over the granary, hay and straw serve as insulators. Under such conditions insect feeding and reproduction continue during much of the winter. Infested feed grains usually are stored in buildings that house animals. The spilled feed grains and littered hay and straw in animal sheds make grain sanitation difficult. In addition, the presence of animals may prevent fumigations of the infested grains.

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## DISCUSSION

F. L. WATTERS. What was the moisture content of wheat treated with pyrethrins-piperonyl butoxide protectant?

D. A. WILBUR. The moisture content ranged between 8.5 and 15.0 per cent.

J. N. TENHET. Has any effect of temperature on the effectiveness of pyrethrum been observed?

D. A. WILBUR. No.



# Die internationale und interkontinentale Bedeutung des Vorratsschutzes

Von FRIEDRICH ZACHER

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Die menschliche Kultur hat sich in prähistorischen Zeiten in weit getrennten Räumen, in allen Kulturkreisen entwickelt. Als solche können wir anführen den mediterranen, den indischen, den zentral — und südamerikanischen, den zentralafrikanischen Kulturkreis. Jeder hat besondere Kulturpflanzen der Acker—, Garten— oder Plantagenwirtschaft und besondere Haustiere entwickelt. Zu jeder Kultur gehört dann auch die Aufbewahrung, Lagerung und Verarbeitung von Produkten. Jede Lagerung hatte aber auch die Entstehung von Lagergut— oder Vorratsschädlingen zur Folge.

In einem Vortrag auf der 12. Mitgliederversammlung der Deutschen Gesellschaft für angewandte Entomologie im Jahre 1952 habe ich darauf hingewiesen, dass die Mehrzahl der bei uns vorhandenen Vorratsschädlinge nicht in Mitteleuropa einheimisch, sondern eingeschleppt und eingebürgert ist, dass aber diese eingeschleppten Formen im allgemeinen wirtschaftlich von viel grösserer Bedeutung sind als die einheimischen Arten.

Dieser Prozess der Verschleppung und Einbürgerung von Vorratsschädlingen hat schon in prähistorischer Zeit begonnen und wird dauernd fortgesetzt und zwar ist anzunehmen, dass er fortdauernd verschärft wird.

Die Kulturkreise waren ja in früheren Jahrtausenden der Menschheitsgeschichte viel schärfer getrennt. Die moderne Entwicklung der Verkehrsmittel hat zur Folge, dass auch die grössten Entfernungen immer bedeutungsloser wurden und die Zeit der Überwindung der Strecke zwischen den Kontinenten von Monaten auf Tage und schliesslich auf wenige Stunden beschränkt werden konnte. So wurde auch den Vorratsschädlingen die Ausbreitung immer mehr erleichtert.

Hinderlich für die Ausbreitung sind natürlich die klimatischen Unterschiede zwischen dem Ursprungsland und dem Empfangsland. Vielfach sind Länder mit gemässigtem Klima Empfänger von landwirtschaftlichen Erzeugnissen aus Tropen — und Subtropenländern. Dann werden die mit den Waren dahin gelangenden Insektenarten sich oft nicht einbürgern können, wenn auch vielleicht vorübergehend halten, vermehren und einigen Schaden anstiften. Ich möchte aber vermuten, dass in den Hochgebirgsgegenden der Tropen noch mancherlei Insektenformen verborgen sind, die auch in gemässigten Ländern als Schädlinge gut gedeihen können. So denke ich z.B. an *Pagiocerus frontalis* (F.) aus Peru, *Pseudomegatoma boliviense* (Pic.) u.a. Die Hochländer der Anden und der zentralasiatischen Gebiete können uns noch manche Überraschung bereiten. Es wäre gut, wenn überall einmal eine Bestandsaufnahme der Speicherfauna vorgenommen würde.

In Mitteleuropa ist jedenfalls der Prozess der Umbildung der Speicherfauna durch Einschleppung und Einbürgern neuer Formen noch im Gange. Daher kann man folgende Stufen unterscheiden:

- 1.) eingeschleppt, auf Speichern und im Freiland eingebürgert und dauernd vermehrungsfähig:  
z.B. *Acanthoscelides obtectus* (Say.).
- 2.) eingeschleppt, auf Speichern eingebürgert und dauernd vermehrungsfähig:  
*Calendra granaria* (L.), *Oryzaephilus surinamensis* (L.), *Ephestia kühniella* (Zell.) und viele andere Arten.
- 3.) eingeschleppt und auf Speichern eingebürgert, nur bei günstigen Wärmeverhältnissen vermehrungsfähig:  
*Calendra oryzae* (L.), *Rhizopertha dominica* (F.), *Sitotroga cerealella* (Cl.), *Aphomia gularis* (Zell.) u.a.
- 4.) eingeschleppt, nur während einer Saison vermehrungsfähig:  
*Callosobruchus chinensis* (L.), *Zabrotes subfasciatus* (Boh.), *Araecerus fasciculatus* (Deg.), *Latheticus oryzae* (Waterh.) u.a.



Die Einschleppung bedeutet aber nicht nur, dass die Schädlingsfauna verändert und mit neuen Arten bereichert wird, sondern auch quantitativ wird die Speicherfauna aufgestockt durch Zufuhr zahlloser Individuen von Schädlingen. In Deutschland waren in den Jahren von 1948 bis 1952 zwischen 40 und 60% des eingeführten Getreides von durchschnittlich 4 Millionen Tonnen im Jahr verkäfert. Ich habe geschätzt, dass im Durchschnitt mit diesem Getreide etwa 2 Milliarden Käfer eingeschleppt worden sind. Die entstehenden Schäden sind gewaltig und sie würden noch viel grösser sein, wenn uns die chemische Industrie nicht vorzügliche Abwehrmittel zur Verfügung stellen würde.

# Methods for the Protection of Woolen Materials Tested by the U.S.D.A. Savannah Laboratory

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## ABSTRACT

Methods of protecting woolens against fabric insects at the Savannah, Georgia, laboratory of the Stored-Product Insects Section, U.S. Department of Agriculture are reviewed. A large number of insecticides have been evaluated as fabric sprays and aerosols and DDT, methoxychlor, Chlordane, lindane, Perthane, and Strobane are being used as temporary protectants. Substitutes for naphthalene to protect boxed woolens are under investigation. Lindane oil solutions applied to the inside surface of wooden storage containers for household use were very effective and long-lasting. A DDT nonionic emulsifiable concentrate known as EQ-53 was developed for mothproofing washable woolens. Wool as well as feathers has a high substantivity for DDT when treated at low concentrates of EQ-53. Placed in the final rinse at  $\frac{1}{2}$  fluid ounce per pound of dry material, a deposit of over 0.25 per cent of DDT on woolens is obtained. Soaps and detergents commonly used for washing woolens do not interfere with the selectivity of DDT in EQ-53 rinses. Originally developed for use in the home, it is ideal for mothproofing washable woolens in commercial laundries, and feathers during mill processing. Preliminary studies show it is also very promising for treating grease wool during scouring. Wool thus treated can be carded, gilled, spun, and twisted and still retain sufficient DDT to protect it. Impregnation of woolen cloth with DDT at the rate of 0.5 per cent by weight was compared with naphthalene crystals at 6 ounces per interstice for the protection of rolled cloth during long-term storage. Damage was present on some of the cloth from the naphthalene-treated stacks at the end of 1 year, whereas the DDT-impregnated cloth was practically free of damage after 8 years' exposure to a heavy insect infestation. A number of "permanent" mothproofers applied during dye bath were compared with the DDT-impregnation treatment to determine effectiveness in protecting woolen cloth during long-term storage.

## INTRODUCTION

Wool is constantly in danger of being attacked by insects from the time it is sheared from the sheep to the time the article made of the wool is discarded or destroyed. The attack may occur while the wool is in storage, during processing, while in transit, while in wholesale or retail channels, or while in the possession of the ultimate owner. Regardless of when or where the damage occurs, the cost is passed to the consumer.

The damage done by fabric insects is enormous. The annual loss due to fabric insect damage in the United States alone has been estimated to be between 350 million dollars (Ferguson, 1950) to 1 billion dollars (Karr, 1955). In addition to this, 66 million dollars are spent for insecticides, cedar chests, and airtight bags; and another 22 million dollars for cold storage and insurance fees for protecting family possessions against insect damage (Hammer, 1956). Still unaccounted are the millions of dollars spent for fabric insect control and prevention by textile mills, warehouses, dye houses, clothing manufacturers, retail stores, and governmental agencies.

A large percentage of the value of goods destroyed by all insects is attributed to fabric insects, yet a comparatively small amount of research money and time is spent on this group. The preventive measures commonly used in the home and in industry today are ineffective, antiquated measures which do nothing but give the users a false sense of protection. In most cases more adequate protection could be obtained at lower cost. An excellent example of this is the recent change by the U.S. Army Quartermaster Corps from the use of naphthalene crystals to DDT impregnation for the protection of woolen cloth during storage. In addition to obtaining a higher degree of protection,

<sup>1</sup> This is one of the field stations of the Stored-Product Insects Section, Biological Sciences Branch, Marketing Research Division, Agricultural Marketing Service, U.S. Department of Agriculture.

an estimated 11½ million dollars will be saved annually in handling and treatment costs (Treichler and Hennessey, 1953). This is an excellent illustration of the high returns that can be obtained with money spent on fabric insect research.

The research on fabric insects conducted by the U.S. Department of Agriculture is performed at the Savannah, Georgia, laboratory of the Stored-Product Insects Section. In addition to investigating the civilian aspects of fabric insect control, the Savannah laboratory has for the past nine years conducted research on the protection of woolens stored in military warehouses. The research work related to the military storage problems has been conducted in cooperation with the U.S. Army Quartermaster Corps and in part under funds allotted by the Department of the Army. The following is a review of the methods of protecting woolens against fabric insects investigated or developed at the Savannah laboratory. Some of the information covered in this paper is already in print, the remainder is being prepared for publication.

MOTHPROOFING SPRAYS

The use of liquid insecticides for treating finished fabrics in the United States is very extensive. A survey conducted by the Insecticide Division of the Chemical Specialties Manufacturers Association showed that 115,110 gallons of liquid sprays and 8,743,351 pressurized units containing insecticide formulations for treating fabrics against insect attack were sold in the United States during 1955 (Anon., 1956). Before the advent of DDT, the fluorides were used almost exclusively as the active ingredients in liquid sprays sold for mothproofing. Today, the chlorinated hydrocarbon insecticides are used extensively in liquid sprays and almost exclusively in formulations packaged in pressurized containers.

The Savannah laboratory has been actively engaged in the evaluation of new insecticides as protectants of woolens against fabric insect damage. Their comparative effectiveness and the resistance of the treatments to washing, dry-cleaning, and aging have been investigated. In Table I are shown the mothproofing qualities of some of the chlorinated hydrocarbon insecticides which are being used or are being considered for use in treating woolens (Laudani and Marzke, 1949; Laudani, 1955). A number of the more promising organic phosphate insecticides presently are being evaluated for their mothproofing qualities.

TABLE I—Mothproofing Qualities of some of the more Commonly Used Chlorinated Hydrocarbon Insecticides.

Name of compound	Minimum effective level	Retentive qualities at 0.5 pct./wt.		
		No. of cleansings before damage occurred		Damage after aging 1 year
		Washings	Dry-cleanings	
	Pct./wt.			
DDT	0.08 to 0.1	1	0	None
Methoxychlor	0.25 to 0.5	0	0	None
TDE	0.25 to 0.5	0	0	None
Toxaphene	0.25 to 0.5	0	0	None
Lindane	0.50 to 1.0	0	0	—
Chlordane	— to 0.5	0	0	None
Dieldrin	0.05 to 0.1	3	0	—
Strobane	0.25 to 0.5	0	0	None
Perthane	0.25 to 0.5	0	0	Very light

PROTECTION OF WOOLENS IN CONTAINERS

Cedar chests and crystals of naphthalene and paradichlorobenzene have been the primary means used for protecting stored woolens and other materials susceptible to fabric insect damage.

CEDAR CHESTS: Regardless of their age, cedar chests are used in the home year after year and are expected to provide the same degree of protection as when they were new. Tests were conducted at Savannah, Georgia (Laudani and Clark, 1954), to determine the efficacy of chests made of red cedar (*Juniperus virginiana*), white cedar (*Chanaecyparis thyoides*), and South American cedar (*Cedrella odorata*) after various periods of aging. Chests of white pine (*Pinus strobus*) were used as checks. These tests showed that cedar vapors have a harmful effect on the viability of the eggs of both the webbing clothes moth (*Tineola biselliella* (Hummel)) and the black carpet beetle (*Attagenus piceus* (Oliv.)) when the eggs were laid by adults enclosed in the chests. However, cedar vapors appeared to have no effect on the eggs introduced after oviposition. Young larvae were much more susceptible than older larvae to the action of the cedar chests, and the full-grown larvae of the webbing clothes moth were more susceptible than those of the black carpet beetle. Exposure of mature larvae in the cedar chests had little or no effect on the pupation and adult emergence of either species, and furthermore, exposed adults mated and laid some viable eggs. Aging was found to have a decided effect on the efficacy of all three kinds of cedar chests tested. Red cedar chests generally produced the highest insect mortality and for the longest period of time as shown in Tables II and III. It should be noted that after aging 30 months all of the cedar chests failed to produce any mortality to black carpet beetle larvae even with a 6-month exposure. Therefore, after cedar chests have aged 2 to 3 years, the protection rendered will depend solely on the woolens being insect-free when stored and on the chests being insect-tight.

TABLE II—Mortality of Webbing Clothes Moth Larvae Exposed in Cedar Chests 1 Month.

Type of chest	Age of chest	Percentage of insects killed	
		Age of larvae	
		4 days	21 days
	Months	Percent	Percent
Red cedar	4	93	74
	26	100	15
	40	—	25
White cedar	4	52	32
	26	14	3
	40	—	21
South American cedar	4	—	77
	16	13	0
	30	—	3
Pine (check)	16	0	0
	26	0	0
	40	—	3

INSECTICIDE CRYSTALS: At the request of the Office of the Quartermaster General, U.S. Army, the effectiveness and duration of the naphthalene crystals treatment used by Quartermaster for the protection of boxed uniforms was investigated. The treatment consisted of sprinkling naphthalene crystals through the uniforms at the rate of 6 ounces per 3.7 cubic foot box (46 g/cu. ft.). A laminated asphalt paper envelope was used in the box to protect the clothing against dust and moisture. The test boxes were stored under natural climatic conditions in insect-infested rooms and breakdown inspections were made at the end of each year. These storage tests showed that effective protection was obtained for only one year, the naphthalene crystals having completely volatilized in that period of time.

TABLE III—Mortality of 70-day Old Black Carpet Beetle Larvae Exposed in Cedar Chests for 1 to 6 Months.

Type of chest	Age of chest	Percentage of insects killed		
		Exposure time in months		
		1	3	6
	Months	Percent	Percent	Percent
Red cedar	4	3	62	99
	20	2	21	98
	24	1	1	60
	30	0	0	0
White cedar	4	4	25	91
	20	1	1	32
	24	0	0	2
	30	0	0	0
South American cedar	4	32	83	98*
	16	3	4	5
	20	0	0	0
Pine (check)	20	3	4	10
	24	0	0	0
	30	0	0	0

\*Mortality after 5 months' exposure.

Because of the tremendous cost involved in replenishing the naphthalene crystals in their large stocks of boxed woolens, the military requested that the investigation be extended to determine whether a longer lasting treatment could be found. Preliminary laboratory tests showed that lindane crystals were very promising for this use. Storage tests in insect-infested rooms with boxed uniforms sprinkled with lindane crystals at 5 grams per cubic foot of box space were started. The naphthalene crystals treatment (46 grams per cubic foot) was used as a standard for comparison. The results obtained at the end of 3 years of storage showed that lindane crystals at the rate used effectively protected boxed woolens against insect infestation and damage for a minimum of 3 years. The lindane crystals still present at the end of 2 and 3 years of storage were 53 and 35 percent, respectively, whereas all of the naphthalene crystals had disappeared by the end of the first year.

The use of lindane oil solutions applied to the inner surfaces of storage containers for protecting woolens is under investigation. The inner surfaces of pine chests made of 3/4-inch stock were painted with lindane oil solution at the rate of 0.1 to 2.0 grams per board foot. Periodically, larvae of the black carpet beetle were exposed in the chests for 1 week to determine the contact and vapor action of the treatments. This was done by exposing the insects directly on the treated surface and in suspended cages. As shown in Table IV, the 0.1- to 0.5-gram treatments produced some mortality by both contact and vapor action but the toxicity of the chests was not sufficiently high to produce adequate protection. However, the 2-gram treatment was producing 100 percent mortality to black carpet beetle larvae by both contact and vapor action 5 1/2 years after treatment.

DEVELOPMENT AND USES OF EQ-53

During the course of investigating the use of DDT for protecting woolens against fabric insects, it was noted that woolen cloth treated with dilute nonionic emulsions picked up considerably more insecticide than the calculated theoretical amount. The great potential of this discovery was immediately recognized and an investigation was started to study the selectivity of DDT by wool, develop a suitable DDT nonionic emulsifiable concentrate, and explore the possible uses for such a concentrate.



TABLE IV—Mortality of Black Carpet Beetle Larvae Produced by Contact and Vapor Action of Lindane Applied as an Oil Solution to the Inside Surfaces of Pine Chests — Exposure Period 1 Week.

Rate of application	Percentage of larvae killed in 1-week exposures				
	Age of treatment				
	1 week	6 months	9 months	12 months	66 months
G/bd. ft.	Percent	Percent	Percent	Percent	Percent
Contact					
0.1	37.5	2.2	2.1	—	—
0.25	100.0	26.4	6.5	—	—
0.5	100.0	57.1	16.4	—	—
2.0	100.0	100.0	100.0	100.0	100.0
None (check)	0	0	0	0	0
Vapor					
0.1	50.0	1.2	1.3	—	—
0.25	92.5	47.5	2.5	—	—
0.5	97.5	44.0	10.0	—	—
2.0	100.0	100.0	100.0	100.0	100.0
None (check)	0	0	0	0	0

DEVELOPMENT OF EQ-53: The basic studies conducted showed that wool had a strong affinity for DDT when treated in a dilute nonionic emulsion bath. It was also found that a definite relationship existed between the weight of the wool being treated and the amount of DDT present in the bath. This relationship was used to establish the rate of application necessary to obtain the desired level of DDT deposit on the treated fabric. The presence of soaps, detergents, water softeners, and the range of pH in wash and rinse water normally used for woolens were found to have no noticeable effect on the rate of DDT pickup and no harmful effect on the treated cloth (Laudani, 1953).

A formulation was developed which would insure a high selective pickup of DDT by wool, safety against damage to the treated cloth, and maximum safety to the user. This formulation known as EQ-53 contained 25 percent of DDT, 10 percent of a nonionic emulsifier of the polyhydric alcohol or alcoholic ether type, and 65 percent of an aromatic hydrocarbon solvent.

USES FOR EQ-53: The first use developed for EQ-53 was the mothproofing of washable woolens. Application studies showed that a DDT deposit of 0.3 percent by weight could be obtained on washable woolens by simply adding one-half fluid ounce of EQ-53 per pound of dry woolens to the last rinse water. This applied to woolens washed by hand, in home-type washing machines, and in commercial laundries. Woolens thus treated were protected against fabric insect damage for a minimum of 4 years when held in dead storage. When used, woolens should be retreated before they are put back in storage. The use of EQ-53 for mothproofing washable woolens was approved and registered by the U.S. Department of Agriculture. Its formulation and the directions for its use were made public at the December 1952 meetings of the Chemical Specialties Manufacturers Association. At the last census, more than 80 firms in the United States and in a number of foreign countries were formulating EQ-53 for mothproofing of washable woolens.

With the advent of stockpiling of feathers for military and civilian use, the protection of feathers against insect damage while in storage became a serious problem. The use of EQ-53 for treating feathers was investigated and it proved very practical and economical. Laboratory tests showed that deposits of DDT at 0.2 percent by weight or higher would satisfactorily protect feathers against insect damage for a minimum of 4 years. It was found that DDT deposits of  $0.5 \pm 0.25$  percent could be obtained

by simply immersing the feathers in nonionic emulsion baths containing 1/2 fluid ounce of EQ-53 per pound of feathers. Mill runs were conducted and it was found that the introduction of EQ-53 in the rinse water at the rate mentioned would produce the desired DDT deposit on all grades of processed feathers (Laudani, Clark, Williams, and Dale, 1955).

Attention was then turned to the important problem of protecting stored raw and partially processed wool. The similarity between the process used for cleaning feathers and scouring wool led to investigations of the possibilities of making scoured and partially processed wool immune to insect attack by treating it with EQ-53 during the scouring process. Laboratory tests showed that the treatment of raw wool with EQ-53 during the scouring process to be promising. Pilot plant treatments were then made by the Sheep, Goats, and Fiber Section, ARS, of the U.S. Department of Agriculture. This series of treatments showed that wool treated with one-half fluid ounce of EQ-53 per pound in the last rinse bowl would have a DDT deposit of approximately 0.3 to 0.5 percent by weight. Furthermore, chemical analyses and biological tests showed that sufficient DDT remained after the scoured wool was carded and combed to protect it against insect damage. Under contract by the U.S. Department of Agriculture, these studies were continued at Lowell Technological Institute Research Foundation, Lowell, Massachusetts. At Lowell, the treatment of raw wool with EQ-53 during the scouring process was further evaluated but particular emphasis was placed on determining the persistency of the DDT deposits as the wool was processed into yarn. The conclusions reached from these studies were that DDT was highly substantive towards wool when treated with EQ-53 in the final rinse bowl of the scouring operation, and that the DDT deposits showed a high degree of persistency through the subsequent processing of the wool into yarn. Table V shows the deposits obtained on the wool treated with EQ-53 at four different rates of application immediately after scouring and after it had been worked through 13 processes from carding to twisting, and winding. It will be noted that all of the processed yarns had considerably more DDT than the 0.1 percent level required for complete protection. These studies showed that it was possible with one simple and inexpensive operation to treat wool with EQ-53 so that it will be protected against insect damage from the time it is scoured to the time it is made into yarn ready for weaving and knitting. Such a treatment eliminates the necessity of the numerous costly treatments normally employed in the warehouses and in the mills to protect scoured and partially processed wool.

TABLE V—DDT Deposits on Wool Treated with Various Amounts of EQ-53 in the Last Rinse Bowl of the Scouring Bath before and after the Wool was Processed into Yarn.

Rate of application	DDT deposit on	
	Scoured wool	Processed yarn
Fl. oz./lb.	Pct./wt.	Pct./wt.
1.0	0.793	0.579
0.75	0.852	0.240
0.50	0.839	0.234
0.25	0.346	0.187

Investigations have been started to determine whether EQ-53 can be incorporated in rug shampoos and rinses for mothproofing woolen rugs and carpets during cleansing. The results of the preliminary tests are very promising. Other possible uses for EQ-53 are also being considered for investigation.

STUDIES ON THE MOTHPROOFING OF ARMY (MILITARY)  
WOOLEN CLOTH

The problem of protecting over 100 million yards of woolen fabrics against insect damage by the U.S. Army Quartermaster Corps is perhaps one of the largest single

undertakings of its kind in the world. The method formerly used for protecting this huge supply of woolen cloth against moth and carpet beetle damage consisted of blowing naphthalene into the stacks of cloth rolls at the rate of 7 ounces per interstice every 6 months. This process was very expensive and its effectiveness was questionable. In 1947 the Savannah laboratory was requested by Quartermaster to determine the degree of protection rendered by the naphthalene treatment, and also to determine the efficacy of cloth impregnated with DDT as a protective treatment against fabric insect damage.

**DDT-IMPREGNATION TREATMENT FOR THE PROTECTION OF WOOLEN CLOTH:** Large-scale storage tests using standard-sized rolls of 14 oz. wool covert and 10½ oz. wool flannel cloth were conducted in insect-infested buildings. The naphthalene treatment was applied to four stacks of 16 rolls each, 4 wide and 4 high. The insecticide was sprinkled between the rolls at the rate of 7 oz. per interstice as the rolls were being stacked. A light-weight canvas dust cloth was placed over each stack. The naphthalene was maintained at a constant level by replenishing the amount which volatilized each month. The DDT-impregnated cloth was treated by the Philadelphia Quartermaster Depot and contained approximately 0.3 to 0.6 percent insecticide by weight of the cloth. Four stacks of DDT-impregnated cloth rolls were prepared in the same manner.

The results obtained showed that naphthalene at 7 ounces per interstice was not sufficiently effective to prevent insect damage to stored woolen cloth, nor was it effective in controlling a fabric insect infestation if one was introduced. Impregnation of woolen cloth with DDT at 0.3 to 0.6 percent by weight is still rendering a high degree of protection after having been continuously exposed to a heavy fabric infestation for 8 years.

A very important secondary benefit is derived from the DDT-impregnation cloth treatment. Storage tests were conducted to determine whether uniforms made of DDT-impregnated cloth would retain sufficient insecticide to protect them against insect damage. The treatment was 2 years old at the time the uniforms were made. These tests showed that the uniforms retained approximately 50 percent of the insecticide (0.22 to 0.30 percent) and this was sufficient to protect the uniforms against insect damage for a minimum of 6 additional years. Therefore, the DDT-impregnation treatment not only protects the cloth during storage but its protective value is passed on to the uniforms thus eliminating the costly treatments which have to be used for protecting untreated uniforms.

The U.S. Army Quartermaster Corps has developed and adopted the DDT-impregnation treatment for protecting its large stocks of woolen cloth. The saving in cost of insecticide and labor has been estimated at 1½ million dollars annually. Quartermaster has developed an ingenious method of treating the cloth during the sponging operation. Instead of sponging with clear water, the fabric is immersed in a DDT emulsion using a concentrate of 25 percent DDT, 2 percent emulsifier, and 73 percent solvent. The amount of DDT left on the cloth is controlled by the pressure of the rollers that remove and recover excess solution. Since the DDT impregnation has been combined with the regular sponging operation, the actual cost of treating fabric is only about one cent a yard (Treichler and Hennessey, 1953).

**COMPARISON OF DYE-BATH MOTHPROOFERS WITH DDT:** As shown in the data which have been presented, DDT is an excellent compound for use as a temporary mothproofing agent. It can be easily applied to finished fabrics as an emulsion or as an oil solution, complete protection can be obtained at extremely low concentrations, its protection is long lasting, and its cost is very low. DDT as a mothproofing agent has, however, certain disadvantages. It crystallizes on the surface of fabrics forming a visible residue on dark colored goods and it is removed by dry-cleaning, repeated washings, and wearing.

There are a number of mothproofing compounds which will withstand a certain amount of dry-cleaning and which will persist on the treated garment through normal wear. However, the cost of these materials is comparatively high, they have to be applied at higher concentrations (2 to 3 percent by weight), and can be applied to fabrics only as dye bath treatments. Maximum permanency in mothproofing is most desirable and, therefore, consideration was given to the use of these dye-bath mothproofing agents for military fabrics on the assumption that their greater permanency could

perhaps justify their higher cost when compared with DDT. At the request of the U.S. Army Quartermaster Corps a storage test was conducted to determine the efficacy of 6 commercial mothproofing compounds to protect woolen cloth against insect damage during storage. DDT was used as a standard for comparison. The U.S. Navy was interested in the evaluation of another commercial treatment and this was included in the test.

The commercial mothproofing compounds were applied during the textile finishing operations in the presence of an agent representing the company producing the compound to advise on the proper application of their product. The compounds and concentrations used are listed in Table VI. The DDT was applied by immersing the cloth in a DDT emulsion bath and then processing the cloth according to the procedure normally used in the sponging operation. Approximately 10 yards of treated cloth were wrapped around wooden spools 10 inches in diameter and 56 inches in length. This produced a roll approximately the same size as one having the standard amount of cloth. Sixteen rolls of each of the treated cloths were prepared in this manner and these were arranged in stacks of 4 rolls wide and 4 high. The only exception to this was the two stacks of Navy cloth which contained 10 and 11 of the treated and 6 and 5 of the untreated cloth, respectively. The stacks of treated and untreated cloth were situated along the periphery of a room measuring 12 x 51 feet. An active infestation of clothes moths and carpet beetles was maintained in the storage room where the cloth is located. At the end of each year, the cloth was unrolled and examined thoroughly for nap and warp damage. Then the cloth was rerolled and placed back under test. The last inspection was made at the end of the 3-year exposure period.

At the end of the third year, the results obtained, as shown in Table VI, showed conclusively that DDT was superior to any of the commercial mothproofers tested for protecting woolen cloth in dead storage. Of the commercial products, the urea compound (2) on wool serge and wool-nylon cloth provided the highest degree of

TABLE VI — The Comparative Effectiveness of a Number of Dye-bath Mothproofers and DDT to Protect Woolen Cloth against Damage as Shown by the Percentage of Rolls Having Various Degrees of Damage after a 3-year Exposure.

Compound		Deposit on cloth	Type of cloth*	Percentage of rolls having indicated damage					
No.	Type			Nap			Warp		
				None	VL-L	M-H	None	VL-L	M-H
Pct./wt.									
1	DDT	0.30	A	56	44	0	88	12	0
2	Urea	2.25	C	19	81	0	38	62	0
2	Urea	2.25	D	6	69	25	75	25	0
3	Silicofluoride	0.49**	B	0	81	26	0	62	38
4	Silicofluoride	0.51	B	0	68	31	12	38	50
2	Urea	1.74	B	0	44	56	0	6	94
5	Phosphonium	2.30	B	0	6	94	0	0	100
6	Silicofluoride	0.51**	F	0	18	82	0	10	90
6	Silicofluoride	0.59**	E	0	10	90	0	0	100
7	Pyridium sulfate	0.21	B	0	0	100	0	0	100
	None (check)	—	B	0	0	100	0	0	100
	None (check)	—	E	0	0	100	0	0	100
	None (check)	—	F	0	0	100	0	0	100

\*Type of cloth used as indicated by letter above:  
A Shirting, 16 oz. OG 108, 90% wool and 10% nylon (U.S. Army)  
B Shirting, 16 oz. OG 108, 85% wool and 15% nylon (U.S. Army)  
C Wool-rayon khaki 7.5 oz. (Canadian Army)  
D Wool, filled serge, drab (Canadian Army)  
E Flannel, blue (dark), 11 oz., 100% wool (U.S. Navy)  
F Melton, blue (navy), 16 oz., 100% wool (U.S. Navy)  
\*\*Deposit expressed in terms of fluoride present.

protection. On wool-rayon cloth, however, it was inferior to the compound containing the mixture of silicofluoride salts (3) and to the hydrofluosilic acid compound (4). The phosphonium (5), magnesium silicofluoride (6), and pyridium sulfate (7) compounds provided very poor protection. The level of deposit obtained with the last mentioned compound was considerably lower than intended and this may have been responsible for its bad showing.

The development of protective measures against fabric insect damage is a most essential phase of entomological research. It is a very badly neglected field of research, especially in the United States. Less is spent per dollar value of susceptible goods or of damage done than perhaps for any other group of harmful insects. This limitation makes the value of the research findings all the more important. It was with this thought in mind that the work done on fabric insects at the Savannah laboratory was summarized and reported in one unit so that it would be more easily accessible to those interested in this phase of entomological research.

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## DISCUSSION

M. H. BREEZE. At what temperatures are lindane-treated cloth and uniforms stored?

H. LAUDANI. The boxed uniforms under test were stored in unheated buildings in Savannah, Georgia. Three months of the year (winter) the low temperature is usually 30 to 35°F. with a high of 60 to 70°F. The remainder of the year the low is 55 to 75°F. and the high is 76 to 100°F. In the building I would estimate the mean temperature to be 55 to 60°F. and 82 to 85°F. in the winter and summer months respectively.

E. A. PARKIN. What was the construction of the boxes in which tests were made with naphthalene and lindane on uniforms?

H. LAUDANI. The boxes were made of wood and were approximately 3.7 cu. ft. in size. They have an asphalt paper liner which when folded over the uniforms makes a fairly tight package.





# New Methods for the Detection and Control of Stored Product Insects

By MAX MILNER<sup>1</sup> and H. H. WALKDEN<sup>2</sup>

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## ABSTRACT<sup>3</sup>

Emphasis on the sanitary status of cereal foods in the United States in terms of freedom from insect and rodent contamination has prompted the development of methods for inspecting commercial grain for internal or so called "hidden" infestation, as well as practical means to remove infested kernels, from bulk grain, and improved grain-treating technics, to control the development of infestation.

Early methods suggested for the detection of internally infested kernels in samples of commercial grain included visualization of egg plugs of certain species by means of stains. These methods fail to indicate stage of insect development within kernels. Other proposals include quantitative counting of insect exit holes, frequently using special optical adjuncts, the grinding-off of grain samples cemented to plane surface in order to reveal their internal condition, and the rendering of kernels translucent by boiling in alkali. Segregation of infested kernels by air blast as well as by flotation in liquids of varying density have been devised as rapid practical preliminary means suitable for commercial use. Electronic aural technics have been developed to detect living infestation not only within grains but also in green plants.

The most objective procedure for infestation detection now widely employed at grain terminals and flour mills for infestation detection is that of x-ray radiography in the range of 15-30 kilovolts using beryllium-window x-ray tubes. This procedure is also used to detect cracking in artificially-dried corn and rice as well as in other applications to cereal processing. Polaroid-Land photographic media have been applied as adjuncts to x-ray inspection of grains thus eliminating the need for darkroom processing of films.

Other approaches which are still in the experimental stage include the use of polaroid lenses and an intense light beam; the detection of infra red radiation produced by the metabolism of the insects within the kernels by a neon light relaxation oscillator; the measurement of the differential scatteration of light waves in infested and in non-infested kernels.

Separation of internally infested kernels from grain cannot be accomplished readily by means of traditional grain cleaning machines. It may be achieved, however, by means of a new device known as a grain spectrometer which projects a stream of grain into air with consequent separation of kernels on the basis of physical differences, thus permitting a strong segregation of infested fractions. Attempts have been made to accomplish continuous separation using high density flotation media such as employed in ore purification.

The increased interest in the prevention of insect infestation in stored grain has necessitated expanded studies on the direct application of insecticidal dusts and sprays to grain as it is harvested or as it goes into storage. The direct application of toxic substances to grain poses a most complex problem, which includes the establishment of effective dosages, the health hazard to man and animals resulting from their use, and the control of the number of treatments to prevent the accumulation of excessive amounts of toxic materials.

A special advisory committee has been set up to review research on this subject and its ramifications, and to advise on the course of further research.

## DISCUSSION

J. A. FREEMAN. Is there difficulty in detecting germ-boring insects by x-rays?

M. MILNER. Difficulty is encountered in detecting germ-attacking insects or those which do not form a void. However, the x-ray does indicate more infestations than other technique, almost invariably.

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<sup>2</sup>Stored-Products Insects Laboratory, Agricultural Marketing Service, U.S. Department of Agriculture, Manhattan, Kansas.

<sup>3</sup>Accepted for publication in *Advances in Food Research*.

J. D. BLECHLY. Assessment of activity or otherwise in structural timber and in experimental material for examination by cutting up is often difficult. We have tried soft rays which involves photography, and also sound detection. Has Dr. Milner any suggestions for such a problem in wood.

M. MILNER. This aspect has not yet been considered.

M. H. BREESE. Have chemicals other than sodium silicate been used in grain flotation tests and why was this chemical eventually chosen?

H. H. WALKDEN. Other chemicals were tested in the early stages of the study. Sodium silicate was chosen because it is readily available, inexpensive, and easily handled. Its specific gravity is easily adjusted and it is non-miscible with the oil-methyl chloroform mixture. Other chemicals no doubt could be found which would be as good or better, but an extensive search for them has not been made.

# The Current Status of Insect Control by Radiation

By CHARLES C. HASSETT  
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## ABSTRACT<sup>1</sup>

*Insect damage to stored products of various kinds, such as clothing, grain, packaged food, etc., is very costly. The use of non-destructive radiation of many kinds has been proposed for the protection of such materials. Experimental evidence shows that ultrasonic vibration, radio-frequency or dielectric heating, X-rays, electron beams, and gamma radiation from radioactive isotopes can be used to kill insects. For large scale treatment, the electron beam from a Van de Graaff accelerator is immediately available and in the near future concentrated fission waste products or spent fuel rods should be practical sources of gamma radiation. The deep penetrating power of the latter favors it for bulk packaged articles. Cost estimates for the process, including shielding, conveyors, and running expenses are from approximately \$20.00/ton to \$1.00/ton.*

## DISCUSSION

S. A. KALOYEREAS. The effect of dielectric heat on the insects at the different stages will depend on the "loss factor" of the insects concerned. The high cost of dielectric heat treatment at present is due to the high cost of the equipment and not to the cost of energy which is very low per ton of material treated.

C. C. HASSETT. 1. The efficiency of dielectric heating is dependent on many factors, e.g. moisture content, shape, and orientation in the field. 2. The use of any method must be decided by the overall costs. Data given in my paper are based on equipment, energy, and other costs, both initial and operating.

J. D. HILCHEY. I wish to express my appreciation for Dr. Hassett's work. We of the Quartermaster Corps (U.S.A.) are obliged to him for his pioneering work. I should like to call attention to one problem which faces us. One anticipated use is for the disinfestation of semi-finished or even packaged products. If this practice is established we must face the difficulty posed by the insect remains left after successful killing action by radiation. I do not believe that any remedies have been suggested up to this time.

C. C. HASSETT. This is a real problem, but the use of radiation can accomplish two things: 1. reduce early infestation by large scale treatment of crops and 2. stop development at a very low level in packaged products.

J. D. BLECHLY. Studies at the Forest Products Research Laboratory in England have indicated that high frequency radiation does not produce differential heating in small larvae, but may do so in larger ones. Attention is being given to the possible use of gamma radiation for controlling infestations of wood-boring insects. Although high dosages are needed to kill these insects, their development can be inhibited or they can be sterilized at much lower ones. Resistance varies at different stages, for instance, mature eggs near hatching need a far higher dosage to inhibit development than ones newly-laid.

G. W. KRANTZ. What is the effect of radiation, at a level approximating 65,000 reps., on the germination of wheat?

C. C. HASSETT. Tests made by Baker, Wiant, and Taboada showed that 10,000 rep. retarded growth of wheat, and that at or above 100,000 rep. the seed germinated but did not grow. At still higher levels, of course, germination would also be prevented. One may compare these results with those of Sparrow on potato irradiation, showing that 20,000 rep. inhibited sprouting.

<sup>1</sup>Published in *Science*, 124: 1011-1012. 1956.





# Recent Developments in Structural Pest Control in the United States

By P. J. SPEAR  
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## ABSTRACT<sup>1</sup>

Structural pest control includes, control of insects, rodents and allied pests that infest dwellings, business and industrial establishments, vehicles and ships. It is estimated that over 10,000 persons are engaged in the structural pest control industry in the United States, providing service which costs about \$100,000,000 per year. Of the several phases of the business it is estimated that about 40% is in general pest control, about 35% in termite control while rodent control, fumigation and other specialties account for the remaining 25%. The pest control industry employs an increasing number of technically trained personnel, including at least 130 graduated entomologists. They provide training, technical service and can accumulate much useful information about pests and pesticides.

Resistance in household pests, principally to chlorinated hydrocarbons, is a most important recent development. It is becoming increasingly widespread in German roaches and in cat and dog fleas and occurs to a lesser extent in brown dog ticks and bedbugs. Control of resistant forms is achieved by intelligent choice of low toxicity organic phosphates or the older inorganic and botanical insecticides. In recent years, the clover mite, *Bryobia praetiosa* (Koch), has become an increasingly frequent pest of structures. Also increasing in importance are the wharf borer, *Nacerda melanura* (L.), and the old house borer, *Hylotrupes bajulus* (L.).

The great demand for housing has resulted in the construction of homes on sites already occupied by numerous structural pests, usually including termites. The fashionable low house built upon a concrete slab at grade level is particularly susceptible to termite attack, and the expense of repairs and treatment in such a building is often much higher than for conventional structures. Industry, government and scientific groups recently investigated the problem and recognized that in addition to sound construction practices, pre-treatment of soil with insecticides is useful in termite control.

Five states have adopted laws regulating the structural pest control industry in recent years, but there appears to be little difference in the practices of the pest control industry in states having or not having legislation. The establishment of tolerances for pesticide materials in or on raw agricultural commodities, resulting in part at least from the general public's increasing desire for freedom from food contamination, has not directly affected pest control operators except in the field of fumigation. The indirect effect of the Miller Bill has been to shift interest in new insecticides to either those having long residual life and low mammalian toxicity, or to those having very short residual life but high toxicity to insects and higher animals. Pest control operators require a material which will remain effective for several weeks and which will provide rapid toxicity to pests.

## DISCUSSION

E. E. KENAGA. What proportion of the 100 million dollars spent for pest control in the U.S.A. can be ascribed to termite control?

P. J. SPEAR. Possibly 35 per cent.

J. D. BLETCHLY. I am interested in Mr. Spear's remarks that the wharf borer and old house borers are increasing. Would he please indicate in more detail the areas involved? Would he also please comment on the significance of attacks by the common furniture beetle, *Anobium punctatum* and *Lyctus* powder-post beetles?

P. J. SPEAR. Wharf borer attacks are chiefly in the state of New York, and in Baltimore and Pittsburgh in buried timber. The majority of old house borer infestations

<sup>1</sup>Published in *Farm Chemicals* 119(11): 42-44. 1956.

occur in the north Atlantic states. *Anobium* is not regarded as significant. Speed of modern building and poorer logging methods probably account for wood-boring insect increase including *Lyctus*.

T. E. SNYDER. I would like to suggest employment of more trained entomologists by industry to assist government agencies in locating introduced insects.

# The Economics of Grain Storage

By STEPHEN S. EASTER

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## ABSTRACT

*Much interest in grain storage in the world in the past ten years has been stimulated by a general food shortage after the war and widespread publicity to emphasize the losses caused by insects, rodents and fungi due largely to poor storage facilities. Much improvement has been effected, reducing the losses through better storage facilities and methods of pest control during this period. However, there has been and still exists a tendency to treat grain storage in its various phases separately according to the training of the individual assigned the responsibility.*

*There is need in a long-term program of grain storage to consider all phases as construction, transport, climate, location, insect control, drying, markets and marketing, grades, etc., in relation to each other before approval of any program.*

*There are three basically different countries with regard to grain storage needs: surplus, deficit and subsistence; each presents a different problem; each presents a separate problem. Only the subsistence country has a truly storage problem. The others require handling more than storage.*

Immediately after World War II there was a very great food shortage in many countries of the world. As grains and legumes furnish most of the basic human food, particular interest was drawn to the losses occurring due to the attacks of insects, rodents and fungi, while the grains were already harvested and in storage.

During the past ten years there has been a great improvement in storage and in the methods to control the losses therein. Nevertheless, grain storage is still a very important problem for many countries.

Following ten years of experience in different countries in connection with grain storage problems it became apparent to the writer that the countries in relation to grain storage problems could be segregated into three distinctly different types: surplus, deficit and subsistence. Most attention has been drawn to the surplus producing countries as Canada, the United States, Australia and Argentina. In these countries the problem is really more of handling and transportation than of storage alone. Installations in these countries must handle many times their static storage capacity. For example, a country elevator in the wheat growing area of the United States is likely to handle fifteen times the actual capacity of the elevator.

In the deficit countries, represented by England and Israel, the problem is, primarily, handling and distribution. Except for a reserve stock for various strategic reasons or insurance against delays in normal deliveries, there is really very little need for true storage.

In the subsistence countries, typified by those of Central America in general, the problem is more truly one of grain storage. Here, the production is roughly that needed for local consumption. The storage capacity is needed from crop to crop. Handling is relatively minor in relation to the actual static storage required and during a given year the quantity of grain handled in a given installation will be roughly the static capacity. Even with two crops being grown in the country, it is unlikely that the quantity handled in the installation will be more than one and one half times the static capacity.

The following remarks will be directed at the subsistence group: Here it must be pointed out that grain storage is being dealt with as an overall problem and not in the light of one phase. Frequently, depending on the technical background of the person involved, grain storage tends to be thought of as insect control by the entomologist; price supports by the economist; construction by the engineer. Generally, there is a regrettable lack of appreciation of grain storage in its entirety where each of these individual items are only small parts of an overall program. The relative importance of any one of these parts of the overall grain storage problem will, naturally, vary from

country to country. It is the purpose of this paper to point out briefly the need to consider many different factors before an attempt is made to plan any improvement in grain storage in countries where requested because of storage losses or high storage costs.

In considering a number of different factors which should be considered, no attempt is made to rate them in the order of importance. Their importance will vary with local conditions. Furthermore, no attempt will be made here to discuss nor recommend methods of insect control as the subject is being covered adequately in that section of the Entomological Congress.

### CLIMATE

Before any direct action can be taken in planning a grain storage system, the climatic conditions must be known and taken into consideration. The requirements for good storage will vary considerably between Central America and the Punjab of Pakistan or the Upper Delta of Egypt. Here, we have extremes from high humidity much of the year to extreme dryness during most of the year. A major consideration in Central America must be adequate grain drying while in the Punjab and in Upper Egypt, the grain is harvested with a moisture content quite ideal for storage.

### LOCATION

If a single installation is planned to improve storage conditions, it is frequently necessary to decide between a location in the center of production or the center of consumption. Obviously, there are arguments for both. The center of the population is usually fixed in the capital city and administration is generally easier here; the grain must ultimately move from the center of production to the center of consumption.

In Ecuador, however, there is a strong argument for leaving the storage at the center of production at high altitudes where the storage conditions are much better than at lower levels where population tends to concentrate.

### SCOPE OF PROJECT

Before much planning can be done on a suitable grain storage system some basic information is needed on the quantity and type of grain which must be stored; the difference in storage needs of wheat, rice and beans is known. A grain storage project may be primarily a means of price stabilization or as some means of defense against speculation in food grain. For example, before the grain storage installation was built in Managua, Nicaragua the fluctuation from the farmer's selling price to the consumer's buying price would vary during the year from 3 to 24 cordobas per fanega. The building of the grain storage plant is reported to have lifted the farmer's selling price to 8 cordobas while the consumer's price was lowered.

The availability of foreign currency for the purchase of materials or equipment not locally available for a grain storage installation may be a determining factor in the size of the original installation. If a complete storage system is contemplated for an entire country it would still be well to start with a single central installation so that experience and training for personnel may be had firsthand under local conditions. Also, no matter how carefully such a project is planned by competent personnel there will be some mistakes made due to unpredictable local conditions.

### TYPE AND SIZE OF CONSTRUCTION

The choice of building material — be it steel, concrete, wood, mud or, other — is primarily an engineering question which can only be determined on the spot not only on the basis of suitability but also on availability. There are many odd ideas regarding the type of materials to be used in grain storage construction and quite often, wishful thinking is involved. Statements have been made, fully unfounded, that such materials as steel could not be used for grain storage. This seems to have been adequately disproven when one sees the various types of steel storage units in the United States and Canada. These odd ideas extend into other phases of grain storage. It has been heard often from self-appointed experts that grain could not be stored in bulk or that bulk grain could not be stored more than 6 to 10 feet in depth. However, such statements usually emanate from persons who had a personal interest in the sale of bags. Because

of local conditions bags are frequently necessary for the transportation of the grain; however, they are costly units of storage and not suited for grain storage. Much of the losses through tropical parts of the world can be traced to the mistaken idea that storage must be done in bags.

If it is accepted that the grain storage is going to be in bags then the storage installation is limited and will require an excessive amount of floor space. If, on the other hand, it is accepted that bulk storage can be used, then comes the problem of the size and number of bins to be included. This, of course, depends primarily on the variety of different basic grains. If many different kinds of grain are involved, it would be logical to limit the improved storage to the basic food grains, standardizing insofar as possible, on those that are of most importance. In Costa Rica, black beans would be sufficient for storage as red, white or other varied colored beans are not popular. The same thing would hold for another country where yellow corn is the staple food. There would be little need here to handicap a storage system by providing space for storage of a minor grain as white corn.

Having accepted bulk storage, the selection of machinery for handling is important. This in turn should be selected in accordance with the volume of the program. The capacity of equipment in the storage unit can be much less and, therefore, at considerable saving in cost than in an installation of comparable size in the United States and Canada, where handling is the prime function. The movement of grain in and out of a storage unit, for example, in Costa Rica, is spread over considerably more time than would be expected in the two above mentioned countries. Some engineers have reported that the basic rule for equipment capacity in the small U.S. installation is to enable it to completely turn over all the grain in five days operation. No such capacity is needed in tropical areas where grain slowly enters storage and should not be disturbed until it is more slowly withdrawn for consumption. The practice of turning grain in cold weather in temperate climates, of course, would serve no purpose in tropical countries except to spread insect infestation throughout the grain.

As mentioned earlier, under "climate", local conditions will determine whether or not a grain dryer must be included and again the type of grain and the method of receiving will determine the capacity of such a dryer. Several years ago, a complete grain installation in El Salvador was purchased without a dryer. Luckily, the installation was not completed until a dryer had been added to the equipment.

The actual size of the installation will also be determined by local factors. In general, it is a good practice to consider starting on a small scale and designing the plant so that expansion is possible if and when needed. In one country where the writer had some responsibility in determining the capacity of the first storage installation, it was found that national pride demanded an installation larger than that possessed by a neighboring country. Actual calculation of the capacity needed indicated that a better job of storage could be done with a smaller installation as there were two distinct crops and it was possible to obtain almost double the static capacity in grain storage per year.

There are considerations regarding the construction which, again, are purely engineering. These would include the prevalence of earthquakes, heavy winds or, poor foundation material.

### GRAIN GRADES

Standard grain grades are lacking still in many countries. Because of this, the storage problem is frequently made more complicated as people insist on receiving their identical stock of grain several years after having placed it in storage. As no grades are established, it becomes virtually impossible to replace any lot of grain with an equivalent grade sometime later. Improvement in the storage system should be a stimulus toward establishing a few simple grades for the major crops.

### VARIETY OF GRAINS

The variety of grains to be stored will, obviously, influence the design of the storage plant. One plan offered for official consideration in Lebanon several years ago, followed the design of a seed grain plant with the many necessary small bins for handling a variety of seed grains. These small bins were not suitable in Lebanon where only two



grades of grain were stored. The design in any country at the starting point can be simplified a good deal if the major storage is restricted as far as possible to a few basic grains.

### CROPS PER YEAR

In some countries, there are distinctly different seasons which produce either two or more crops of a single grain or the harvest time varies for different grains. In planning a grain storage system, this must be taken into consideration as it may be possible to use the same storage space twice in one year. Actually, relatively little storage space is needed in Indonesia where there is almost a continual harvest of rice.

### TRANSPORTATION

The type, cost and availability of transportation may be a very important factor in determining, either the location or the size of a grain storage installation. With excellent, cheap transportation, it may be found to be more economical to store grain in a large central installation even though this may require some reshipment to the areas of consumption. Obviously, no decision could be made without a knowledge of the availability and cost of the transport to compare against the advantages of a large central storage installation.

### PERSONNEL

Along with all the factors, those enumerated above included, which will help to determine the details of the grain storage system, attention must be given to the availability of trained personnel or practical schooling for the people to be responsible for the grain storage. Poor management itself in either improved storage or existing storage does much to contribute to various losses, not only from insects, rodents or fungi, but also in general inefficiency of operations. A number of examples of poor management will be given to illustrate this.

The time of purchase of supplies to go into storage may be very important. In Lebanon, wheat is traditionally purchased from Syria, where the harvest is usually August through October when the grain is extremely dry. Purchases by Lebanon are not timed for shipment during this dry season but are more likely to occur in December or January when rains are quite frequent; consequently, instead of having a good dry grain of 10 or 11% moisture to go into storage, grain is received with increased moisture content, at times, too high for good storage.

Some of the problems in grain storage and transport could be partially solved by the purchasing country. Iraq, traditionally exports barley which has been harvested by winnowing. One engineer studying this problem in Iraq reported that the major problem of the exporters in Iraq was the difficulty of adding the 6% allowable trash to the clean barley before shipment. There was a disadvantage and direct loss to them in shipping clean barley. In a shipment from another country to Genova, Italy in 1947 the wheat on arrival was found to contain 12% pebbles which was, to say the least, quite a waste of shipping space.

In a number of storage installations visited in various parts of the world, it was evident that while some effort had been made to control losses from various pests, there was no authority given to a technician to actually accomplish this. This was evidenced in one country by the addition of badly infested beans to a partially filled bin which had been fumigated the day before. The protests of the technical man had been overruled by the manager who had no appreciation of the excessive potential losses to be caused by the insects present.

Many examples of poor management could be cited; a few outstanding ones will suffice for the purpose here.

In one Central American country it was noted that while excellent bulk bins were available but empty, badly infested bagged material was being carried on the warehouse floor space. The cost of labor on bag handling was high, insect control was virtually impossible under the circumstances and the bag rental ran high.

In Burma and British Honduras, good storage space was observed being used for storing low grade, badly infested, rice bran while valuable milled rice or corn had no

adequate storage space at all. In both these countries, the rice bran had been priced too high for the market.

In Thailand, in 1953, a rather serious rice storage problem developed because export sales stopped but rice milling continued until every available storage spot had been filled with the milled rice. Milled rice is infinitely more susceptible to damage by insects than unmilled rice.

### COST OF INSECT CONTROL

The cost of insect control, because of lack of facilities, may be unjustifiably high. This is forcibly shown in India in the government controlled stores of grain. The losses from insects are negligible but the cost of preventing such loss is extremely high because of the lack of proper facilities in which to store and treat the grain. In other places, the lack of simple sanitation may contribute greatly to rapid infestation and resultant serious losses in the stored grains. This is particularly true where old stocks of infested grain are not promptly disposed of. Frequently the management lacks the authority to condemn or sell such grain even though quite often it would be much cheaper to throw it away than to keep it in the warehouse as a source of infestation.

It is obvious that the conditions from country to country vary greatly with many factors at wide variance with conventional practices in the United States and Canada. It should be equally obvious that in covering the broad subject of grain storage in the subsistence countries, no one person nor any group of persons, no matter how competent, can plan an adequate grain storage system without careful study in the country concerned including travel outside the capital cities.

### DISCUSSION

G. H. SPITLER. Do you see the possibility of a universal grading system being adopted?

S. S. EASTER. No. I tried to emphasize the need for some simple system within a given country.



# Residual Insecticides, Tolerance Limits and Stored Foodstuffs

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## ABSTRACT

*Particularly in hot climates, vigorous hygienic measures cannot fully cope with insect infestation in stored produce and the use of insecticides becomes a necessary complement. In their use, however, the consumer of foodstuffs must be protected from harm and the laying down of tolerance limits by toxicologists is a great help to the entomologist in determining the best ways of using insecticides. Very few species can be controlled by insecticides uniformly distributed in foodstuffs at dosages corresponding to the tolerance levels and the entomologist must exercise his ingenuity to work out methods of applying local higher dosages where the insects are likely to come in contact with them.*

*Not to be overlooked, however, are the various factors which operate to protect the consumer even after an initial dose in excess of the tolerance limit has been necessarily applied to a commodity. These factors concern cleaning, processing, and cooking; loss by handling and volatilization in storage; the proportion of the diet containing contaminated foodstuffs; the time needed at low levels of intake to provoke symptoms; and the increasing purity of some preparations.*

*In line with the thoughts expressed in this paper recent amendments have been made to the U.K. Code of Practice (which states tolerance limits of 7 p.p.m. DDT and 2.5 p.p.m. gamma-BHC for stored foodstuffs) to permit initial dosage at rates above the limits provided that the limits are not exceeded at the time of consumption.*

For very many years research has been prosecuted into the protection of growing crops against insect and fungal infestation, but surprisingly little attention has been paid until fairly recently to the problems of conserving harvested crops in storage. The harvested crops I have in mind are those which, together with certain manufactured materials, can be included in the term "stored product"; these comprise crops or their products that can be kept wholesome in suitable storage for a year or more and that have a moisture content during storage of about 20% or less.

Among the chief agents of deterioration of products in store are fungi and insects (including mites). In most parts of the world and for most products, the fungi can be controlled by reducing the water content of the product a little below that at harvest, whereas it is rarely practicable or economic to reduce the water content to and maintain it at a level low enough to prevent insect infestation. The control of insects therefore presents the more serious problems.

The most commendable method of protection of stored products against insect infestation is hygiene in the storage place but in warm climates hygienic measures, however earnestly carried out, are often quite unable to cope with the infestation pressure of the attacking insects. Hygiene must be then supplemented by other control measures, usually fumigant and contact poisons.

To narrow the subject of my paper, I propose to confine myself to consideration of the contact insecticides, especially DDT and BHC.

In agriculture, the application of contact poisons at least a week or two before harvest enables reliance to be put on loss of insecticide through weathering, "dilution" by growth of the crop, or detoxification by the plants. In stored product entomology, these factors do not operate, although there may be some loss by volatilization of certain insecticides, such as lindane. Cleaning processes cannot be relied upon to remove all traces of insecticides and in some countries grains may be ground and eaten without any preliminary cleaning.

In countries with a high standard of hygiene, there is nowadays a movement to reduce adulterants in foodstuffs so far as possible; and insecticide residues must be considered undesirable constituents. If insecticides are therefore to be used in places where foodstuffs are stored or processed, one of the serious responsibilities laid upon

those of us who in any way give advice, directly or indirectly, is to ensure no harmful contamination of the produce. I propose to leave out of consideration those forms of taint that are susceptible to organoleptic perception and to discuss only those levels of contamination that may involve some toxicological risk. Contamination at a level likely to induce acute toxicity can never be permitted and any foodstuff so treated must immediately be condemned. We need therefore concern ourselves only with contact insecticides at low concentrations in foodstuffs involving the possibility of chronic oral toxicity.

There is a maximum safe level of intake of any poisonous substance at which the concentration of toxic materials in the body can be tolerated indefinitely without harm to any organ. The experimental determination of this level of intake involves tests on animals extending over many months or years and the difficulties of such tests have been well described by Barnes and Denz (1954). When a tolerance level can be fixed by the toxicologist, it is of immediate value to the applied entomologist for working out limiting dosages in many forms of insecticidal treatment, especially if the chemist can provide data on the residues of insecticides found in foodstuffs after exposure to known conditions of treatment and storage.

### EXISTING TOLERANCE LIMITS

The little information available upon tolerance limits has been mostly recorded by the European Plant Protection Organization (1953). Zero tolerances for DDT and BHC are set by Algeria, Belgium, the Netherlands, and Switzerland. Up to 20 p.p.m. DDT is allowed in Denmark to protect grain intended for animal feeding. France allows up to 5 p.p.m. lindane to be applied to harvested cereals and pulses, but not more than 1 p.p.m. must remain in flour.

In the U.S.A., tolerances under the Miller Bill for insecticides applied after harvest are now beginning to be published. Too few are yet available to permit useful general comment, especially as they are applicable to specified products only. It is, however, perhaps worth drawing attention to the declaration of tolerances of 3 p.p.m. for pyrethrins and 20 p.p.m. for piperonyl butoxide because in other countries these substances may be more freely used on stored foodstuffs. The seemingly low levels of these tolerances are presumably dependent on the minimum dosages considered necessary for the protection of grains in the U.S.A. rather than on toxicologically safe levels.

In the United Kingdom tolerance limits of 7 p.p.m. DDT and 2.5 p.p.m. gamma-BHC were laid down in 1950 and it was recommended that practical dosage should not exceed the tolerance limits. These recommendations exist as a "Code of Practice" which has no legal status but is accepted and honoured by all responsible persons in the United Kingdom. The Code of Practice is also in general usage throughout the British overseas territories except Kenya where 1 p.p.m. gamma-BHC is the tolerance limit, apparently adopted to avoid the possibility that local contamination in excess of 2.5 p.p.m. might arise through poor mixing of insecticidal dusts into grain, etc. In Kenya, however, up to 12.5 p.p.m. gamma-BHC may be applied to cob maize in cribs (Kockum, 1953). During 1956, some of the qualifying statements in the Code of Practice have been revised so that the tolerance limits may be exceeded in the treatment of produce to control insect infestation, provided that the produce when prepared as food contains no more than the stated limit. In addition, BHC for application to food and food stores should be of lindane quality.

### EFFICACY OF INSECTICIDES AT TOLERANCE-LIMIT DOSAGES

It is obviously of practical interest to know the insecticidal value of insecticides applied at or below dosages corresponding to the respective tolerance limits, e.g. when dusts are admixed with grain or pulses. DDT at 7 p.p.m. on peas or beans will protect them against the Bean beetle, *Acanthoscelides obtectus*, and the Cowpea beetle, *Callosobruchus chinensis*, (Parkin & Bills, 1955a). From indirect evidence (Parkin, 1953) this dosage should also be effective against Flat Grain beetle, *Laemophloeus* spp., and the Coffee Bean weevil, *Araecerus fasciculatus*. Control of other common pests such as Granary weevils, *Calandra* spp., and Flour beetles, *Tribolium* spp., requires much higher doses. Similarly, gamma-BHC mixed with the product at 2.5 p.p.m. will



control *A. obtectus*, *C. chinensis*, and *Laemophloeus* spp.; it is also effective against the Granary weevils, *Calandra* spp., the Lesser Grain borer, *Rhyzopertha dominica*, and the Groundnut beetle, *Caryedon fuscus*, (Parkin & Bills 1953, 1955b; Parkin & Scott, 1956). Other species such as the Saw-toothed Grain Beetle, *Oryzaephilus surinamensis*, are known to require much higher doses for their control (Parkin & Bills, 1952).

There is thus considerable specificity in the susceptibility of stored product insects to DDT and gamma-BHC; at dosages corresponding to the U.K. tolerance limits, a few species can be controlled but many certainly cannot.

### THE CONTAMINATION OF FOODSTUFFS BY INSECTICIDES

Contamination may arise directly from application of an insecticide to a product or indirectly from transfer of insecticide to produce from deposits on containers, warehouse surfaces and so forth. Much more information than is now available is needed on the transfer of insecticides from treated surfaces etc. and on their retention during industrial and domestic cleaning and processing of stored foodstuffs: domestic cleaning is here intended to include washing, winnowing etc. as often practised in native communities, processing similarly involving grinding by pestle and mortar or by hammer mill, and cooking.

Butterfield, Parkin & Gale (1949) showed that foods stored in jute sacks impregnated with DDT became more contaminated the smaller their particle size, the greater their fat or oil content, the higher the dosage of DDT, and the longer the storage period; contamination can also be presumed to increase at higher temperatures of storage. The levels of contamination found were too high for the use of DDT-impregnated sacks to be recommended, except for whole grain. Confirmation of the excessive uptake of DDT by flour was obtained by Atkins & Greer (1953). Parkin (1954) has also given some information on the levels of contamination of wheat exposed in bulk or in bag to DDT sprays, dusts, wettable powders, and smokes.

Because of its volatility, lindane can be expected to cause greater or less contamination according to the circumstances of treatment and storage. Atkins and Greer (1953) recorded a surprisingly high transfer of mixed isomers of BHC from sacking to flour in six months. With a comparable dosage of lindane (50 mg./sq. ft.), Pingale & Majumder (1955) found no detectable contamination of wheat flour during 12 months storage. Using sesame oil as a synergist for lindane Pingale (1955) was able to reduce the effective dosage of lindane even further. A low level of contamination of flour from lindane spraying of jute or paper bags has also been claimed by Bernfus (1955).

Four other factors are often brought into discussions on the contamination of foodstuffs: (a) non-uniformity in mixing, e.g. dusts in grain, (b) unwitting or unnecessary repetition of treatments, (c) carelessness leading to overdosing, and (d) the use as food of surplus, heavily treated, seed stocks. The solutions of the problems involved fall more within the realm of administration than science.

Non-uniformity of mixing is of little import, as it is scarcely likely to lead to chronic toxicity, although in extreme cases acute effects might be evoked. Repetition of treatment is a more serious risk but could be reduced by the use of labelling or certification, including the use of specially marked bags. There is no cure for the human failing of carelessness except instruction and supervision, but it is a cause of risk to us one way or another in almost every moment of our lives. The use of seed stocks should present little hazard, since the heavy treatment is usually well known and often easily visible and waste of such surpluses can be avoided by cleaning and dilution with untreated material. The risk is clearly highest where insecticides are used by uneducated individuals and communities and can be reduced only by education and supervision.

### FACTORS REDUCING THE TOXICOLOGICAL RISK

The cleaning of grain etc. prior to milling is a generally recognized factor which helps to protect the consumer, but there are a number of other factors making sometimes small, but nevertheless definite and complementary, contributions to safety.

**LOSS DURING STORAGE:** During commercial handling there are sure to be slight mechanical losses especially of insecticidal dusts and wettable powders, but the chief

loss in storage occurs from volatilization; this is particularly the case with lindane. Zeumer & Neuhaus (1953) and Maltha (1954) found a marked reduction in the lindane content of wheat stored for a few months and Ciferri (1954) in laboratory experiments was able to show a big fall in concentration of lindane in 48 hr under conditions of good ventilation. The rapid loss of lindane from surface treatments under tropical conditions is brought out by the experimental results of Duerden *et al.* (1956).

**CLEANING BEFORE CONSUMPTION:** In the more advanced countries, all types of stored foodstuffs likely to be treated after harvest with DDT or lindane will be commercially cleaned before processing and the risk to the consumer, if it exists, will be very small indeed. In more backward countries and communities, a product may be eaten without cleaning. In tropical countries, the most effective use of insecticides such as DDT and lindane would be in the admixture of dusts with grains and pulses. If reasonably uniform distribution of dust is required with simple mixing methods, about 200 g. of powder must be added to 100 kg. of product; seed dressing machines can cut the dose to about 50 g./100 kg. Good distribution is aided by the use of a base dust such as kaolin, which adheres well to and whitens grains. The dustiness of the product then invites cleaning by washing, sieving, rubbing with a cloth, etc., but for bulk cash crops interferes with inspection and grading.

An interesting problem is posed by the treatment of oil seeds which are not usually cleaned before pressing out or extracting the oil, in which the insecticides may be fairly soluble. Hayward (1951) sprayed two commercial stacks of bagged groundnuts in Nigeria with wettable powders at the very heavy doses of 725 mg. DDT and 305 mg. crude BHC (15% gamma-isomer) per square foot respectively. After six months storage under tarpaulins, nuts from the outside bags were pressed and the resulting oil and cake found to contain respectively 27 and 5.5 p.p.m. DDT and 14 and 6 p.p.m. BHC (total isomers). Assuming practical dosage rates and the mixing of inside and outside bags from the stack before or during processing, Hayward concludes that in practice any residue in the oil and cake should not exceed the U.K. tolerance limits.

Grain treated with 50-100 p.p.m. DDT has been shown to retain about 10 p.p.m. after it has passed through the normal mill cleaning processes prior to grinding [Zinkernagel *et al.* (1946), Leggieri (1949), Zeumer & Neuhaus (1953), Parkin (1955)] and this figure will be further reduced by loss with the bran during milling. In view of its well known propensity for storage in the body fat and excretion in milk, DDT should not be recommended now for admixture with grain but the results from the grain-cleaning experiments are useful in indicating what may happen with other insecticidal dusts. Almost irrespective of the insecticide used, a difficulty of grain dusting is the ultimate disposal of the heavily contaminated cleanings and bran which normally have a considerable market value.

Viel & Rohart (1952) and Maltha (1954) have shown with lindane-dusted grain that a large proportion of the dust is removed during the ordinary cleaning processes and Maltha has demonstrated, in addition, that most of what remains is retained during milling by the bran and wheat feed, [see also Zeumer & Neuhaus (1953)].

**PROCESSING AND COOKING:** Starting with barley dusted with 100 p.p.m. of DDT, Klaushofer (1952) investigated the losses of insecticide following steeping, germination, kilning, and brewing. Most of the DDT had disappeared by the time the malt had been kilned and the remainder was completely destroyed during brewing.

Leggieri (1950) found the DDT content of bread was about one-half to one-third that of the flour (8 p.p.m.). Zeumer & Neuhaus (1953) starting with flour containing 6-8 p.p.m. DDT or 1-2 p.p.m. lindane, obtained bread with less than 0.2 p.p.m. of either insecticide and suggested that the DDT was lost by decomposition and the lindane by steam distillation. Winteringham *et al.* (1950), on the other hand, found 11.2 p.p.m. bromo-DDT in bread baked from flour containing 14.6 p.p.m. of the compound. Similarly, Carter *et al.* (1948) recorded no material loss of DDT from meat whether the meat was roasted, broiled, braised, fried, or pressure-cooked.

The firm J. R. Geigy A.G., Basel, reported (Lefèvre, 1950) that boiling white haricot beans, dusted with 100 p.p.m. DDT, for 1½ or 3 hr in open or closed vessels

left only 2-10 p.p.m. DDT, most of the insecticide being lost by entrainment in the steam. Loss of DDT while boiling an acetone dispersion in water has also been recorded by Cutkomp (1947). The importance of food extractives on the stability of DDT during cooking has been demonstrated by Tressler (1947) who showed that DDT was stable in distilled water when heated at 100°C. for 4 hr in a sealed tube but suffered 20-30% decomposition in 20 min. at 100°C. when processed with various fruits.

In considering contact insecticides for the preservation of most oil seeds in store, e.g. groundnuts, it is likely that the oil will undergo severe processes of neutralizing and deodorizing, and hydrogenation if converted to margarine, each of which will tend to reduce the concentration of the insecticide to an extent not yet investigated.

**PROPORTION OF WHOLE DIET:** In chronic toxicity tests animals are often given insecticides mixed with the diet at known concentrations. Tolerance limits however apply to each individual item of the diet and unless the increasing use of insecticides ultimately leads to contamination of all the main articles of diet such as meat, milk, fruit, vegetables, bread, etc. a considerable safety factor is introduced here. Nevertheless, this factor might be very small for certain communities living on restricted diets, e.g. rice, millets, maize, pulses.

**CHRONIC TOXICITY:** As has been mentioned earlier, tolerance limits relate to the ingestion of insecticides over long periods of time and are usually founded upon animal feeding experiments extending over six months to two years or more. There should be no risk attendant upon the consumption of doses just above the tolerance limit for a few days.

Vast quantities of DDT and BHC are now being used throughout the world for the control of insect pests on edible crops, before and after harvest, and it seems that, at least in the U.S.A., a minute daily dose of DDT is not rare among those eating in restaurants (Price, 1954; Walker *et al.*, 1954). None the less, there seem to be no published authentic cases of chronic poisoning caused by ingestion of DDT or lindane (McGee, 1955), nor published records of seizures of foodstuffs because of excessive contamination by contact insecticides like DDT and lindane. The daily ingestion by human volunteers of about 200 times the likely intake of DDT in the average diet has, over nearly a year, evoked no detectable clinical symptoms (Hayes, 1955; see also Fennah, 1945). In this connection, we must not overlook the obscurity of the symptoms (hyperexcitability, headaches, transient giddiness, digestive disturbances) likely to indicate the early stages of chronic poisoning from chlorinated hydrocarbon insecticides such as DDT and BHC, but conversely the prolonged period of slight malaise likely to precede any serious effect gives plenty of time for investigation of the cause and a good chance that the intake of the toxicant may cease for some reason and spontaneous recovery follow.

**PURITY OF INSECTICIDES:** The U.K. tolerance limit of 2.5 p.p.m. for gamma-BHC was founded on tests with crude BHC containing about 12.5% of the gamma-isomer. It has since been established that the alpha and beta-isomers are chronically some four and ten times respectively more toxic than the gamma (Fitzhugh *et al.*, 1950). The recent insistence upon the use of lindane-quality preparations where food stores are involved therefore increases the safety factor with this insecticide.

## GENERAL DISCUSSION

Everybody will agree that there is no justification for insecticidal treatments, however effective, if a real hazard results to the consumer. Equally, there is no justification, in this world of daily risks to us all, to enforce the total exclusion of insecticides: some can clearly be put to good use in preserving food stocks without involving any real risk of contamination.

Basic information on the chronic toxicity of promising insecticides must be given by toxicologists and this, if expressed as a tolerance limit, can form a valuable basis for the determination of safe usage in practice. This toxicological information, however, needs to be considered in the light of data upon the pick-up of insecticides by different articles of stored produce under various conditions of storage and the factors that

govern the extent of uptake. This falls to the chemist to investigate but information is at present very scanty and much urgent work on levels of contamination arising under practical conditions of treatment waits to be done. The real importance of some of the safety factors already discussed also needs clarification by more chemical research. The responsibility rests with the entomologist, however, to integrate toxicological and chemical evidence with knowledge of relative susceptibility of the pest species and the expected history of the produce after treatment and to select the method of application likely to kill the highest proportion of insects with the lowest possible risk of contamination of the product. His is also the responsibility for assessing the risk involved in possibly exceeding the tolerance limit during initial dosage, compared with the probable loss of foodstuff which will follow inadequate treatment or no treatment with insecticides. When control can be obtained without the use of insecticides, this must obviously be the preferred method.

In an advanced country producing a surplus of staple foodstuffs, tolerance limits will tend to be set low and their interpretation to be strict, partly because of public prejudice against any contamination of foodstuffs with chemicals and partly because no food shortage is felt if insect-infested produce is diverted to animal feed or to export. In a less advanced country, however, where public prejudice about foodstuffs is less evident and where occasional years of serious crop failure can lead to famine, the threat of loss, through insect infestation during storage, of 50 per cent or more of the reduced crop (Parkin, 1956) can lead to a different outlook on the slight risk of chronic toxicity to the consumer that might arise from successful preservation of the harvest by the intelligent use of insecticides. We must therefore expect that tolerance levels will not necessarily be the same in all countries; and within some countries there may be a need for greater flexibility in interpretation than in others. Considerations of the latter kind have led the United Kingdom recently to review the Code of Practice recommended for use in its overseas territories and to alter it to allow the initial contamination of the foodstuff by DDT or lindane to exceed the stated limit if it can be shown, or reasonably expected, that (a) removal of insecticide by washing, screening, or similar processing, (b) loss of insecticide by volatilization during the storage or processing, or (c) dilution of insecticide by mixing treated with untreated produce, will reduce the level in the particular item, when prepared as food, to or below the stated limit.

I have tried in this paper to discuss the background of tolerance limits as it is seen by an entomologist who must constantly bear it in mind in making recommendations for stored-product insect control. While I find myself in sympathy with Lehman's (1954) plea for conservatism in estimating the hazards of pesticidal residues and consequently urge that the safety factors I have discussed should, so far as possible, be maintained as a safeguard for the consumer, I also feel that flexibility of interpretation within reasonable limits should be exercised where the situation warrants it.

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# Protection of Stored Grains with Pyrethrins and Piperonyl Butoxide

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## ABSTRACT

Grain protectants containing pyrethrins and piperonyl butoxide were reported upon at the Ninth International Congress of Entomology at Amsterdam. The present report concerns the extended use of the Pyrenone dust formulations, also the more recent but officially accepted Pyrenone liquid protectants, each of which is used for prolonged protection of stored grains from insect damage. Either type of protectant is conveniently and economically applied to the stream of grain as it is being put into storage.

A new innovation that favors the use of liquid protectants in the larger storages has been the development of a highly concentrated Pyrenone 75-7.5 O.F., one in which no mineral oil is added. This "oil free" base is combined by the manufacturer of the finished concentrate with an officially endorsed emulsifier. Such a complete formula is then entirely acceptable to the governmental agencies concerned, and needs only to be diluted with water for application to grains.

A milestone has been reached in official recognition and acceptance of these protectants by governmental agencies in the United States. A tolerance by the Food and Drug Administration grants the use of 20 parts piperonyl butoxide plus 3 parts pyrethrins per million parts of grain. These amounts are in excess of the quantities required for a normal storage period of nine months, and enough to permit sufficient amounts for obtaining longer protection periods from a single treatment. Other than the official tolerances which serve as an acknowledgment of the safety of these ingredients, the United States Department of Agriculture has for the past two years recommended in Leaflet No. 345 the use of these ingredients for the protection of farm stored wheat. Following these two official endorsements, it is highly significant that a third agency responsible for the storage of government owned grains has purchased protectants made of pyrethrins and piperonyl butoxide for use on government owned grains in the United States. The successful use of these protectants is arousing interest in different lands where grain insects continue to inflict heavy losses.

Five years ago it was the writer's pleasure to report to the 9th International Congress of Entomologists at Amsterdam on some practical field trials with powder protectants containing pyrethrins and piperonyl butoxide for the protection of stored grains. Since then, a lot of progress has been made and some new milestones have been reached. It seems desirable to list the most important points in the same order in which the developments were made.

(1) A powder protectant is now used in different foreign countries and there are recommendations from entomologists in the principal grain producing states. In addition to these, a wheat protectant is in use and is recommended in United States Department of Agriculture Leaflet No. 345.

(2) A spray treatment containing the same active ingredients, together with a satisfactory emulsifier, is being used successfully on different stored grains. It was intended primarily for the larger grain storages but it is finding good acceptance on farms. Both the sprays and dusts, when properly prepared in suitable formulations and properly applied, are finding increased use.

(3) For various grains, the U.S. Food and Drug Administration officially allows a tolerance of 20 parts piperonyl butoxide and 3 parts pyrethrins per million parts of grain. These amounts are more than those needed for obtaining two years protection of grains from insect damage.

(4) For peanuts, copra, cocoa beans, beans, oats, flax seed, cotton seed and a variety of fruits, an official tolerance has been allowed for 8 parts piperonyl butoxide and 1 part pyrethrins per million parts of these commodities. The latter tolerance is based on the need for killing adult insects with space treatments at intervals of 2 weeks during the warmer months of the year.

The developments mentioned represent pioneering efforts because there was no previous clearance of a pesticide for post harvest uses. The findings that justified official clearances resulted from a continuing grain insect program of research and development for the past ten years. In the conduct of the work progress reports were made as the results were obtained. These were given during visits to groups of key men of the government scientists concerned. At such meetings, specific suggestions were received from the cooperating specialists on future explorations and at the same time these men were able to set up their own experiments for checking the results. By the time the program was completed, there was a definite pattern for similar investigations of the future. It is understood that these methods developed from actual use will be followed in the future for determining the suitability of any candidate pesticide that is intended for use on raw agricultural products that may serve as foods of man or feeds of animals. Because of the importance of the investigations that led to the approval of pyrethrins and piperonyl butoxide for the protection of stored grains, the present paper gives some highlights of the developmental work.

### IDENTITY AND FORMULATIONS

Piperonyl butoxide is the commonly accepted name for (butyl carbityl) (6-propyl piperonyl) ether or (3,4-methylenedioxy-6-propylbenzyl (butyl) diethylene glycol ether. Technical piperonyl butoxide contains not less than 80% of (butyl carbityl) (6-propyl piperonyl) ether and not more than 20% of related compounds.

Pyrethrins are the insecticidally active principles of pyrethrum flowers, the species now used commercially being *Chrysanthemum cinerariaefolium* (Treviranus) Boccone; these are designated as Pyrethrins I and II and Cinerins I and II. In most insecticidal compositions, pyrethrins are now used in the form of extracts made by solvent extraction of pyrethrum flowers.

A representative formula for a grain protectant powder consists of: Technical piperonyl butoxide 1.00% and Pyrethrins 0.06% (T-414B). In its manufacture, a concentrated dust base is mixed at the rate of 25% with 75% fibrous talc.

A representative liquid grain protectant spray is made from a base (OF 75-7.5) that contains no added mineral oils. From this base, an oil free emulsifiable concentrate 60-6 (T-647) is prepared by the manufacturer of insecticidal sprays for dilution with water. Such a concentrate contains piperonyl butoxide 60%, pyrethrins 6.0%, emulsifier MYRJ 45 (polyoxyethylene 8 stearate) 20%, and other pyrethrum extractives 14%.

### RATES OF APPLICATION

The grain protectant powder mentioned above is evenly applied to grains as the grain is being put into clean bins. It is used at the rate of 80 to 100 lbs. per 1000 bushels. The 80 lb. rate is ample for most storages, but for difficult situations that favor development of grain destroying insects, the 100 lb. rate is sometimes advisable. On shelled corn which weighs 56 lbs. per bushel, an 80 lb. rate of application results in an initial calculated residue of 14.3 ppm piperonyl butoxide, while the 100 lb. rate gives a similar residue of 17.9 ppm of piperonyl butoxide and the accompanying pyrethrins. The theoretical initial pyrethrins deposits may be calculated by applying the ratio of the two ingredients in the formula to these amounts of piperonyl butoxide. On the surface of the grain the usual procedure is to apply twice the normal amounts of the protectant. This is for added protection against any incoming insects.

The oil free emulsifiable concentrate 60-6 is ready for use as a protectant spray when it is diluted with 29 equal volumes of water, which gives a spray containing 2.0% piperonyl butoxide and 0.2% pyrethrins. It is applied to the stream of clean grain as it goes into the bin at a uniform rate of 5 gals. per 1000 bushels of grain. For shelled corn this gives a calculated initial deposit of 15.2 ppm piperonyl butoxide and 1.52 parts pyrethrins per million parts of the treated corn.

The usual time for applying either the protectant powder or spray is just after harvest. Either may be applied to clean grains at any time of the year as the grains are turned or moved into new bins. Either is effectively used following fumigations, if the fumigant kills the hidden infestations. These protectants are not recommended for infested grains or as replacements for fumigants.

For grains in PMA metal bins the oil free emulsifiable concentrate 60-6 is also diluted with 29 volumes of water for use as a surface spray at 0.8 quarts per 100 square feet of surface of the grain for the control of moths.

As a protectant of seed corn and other large seeds from insect damage, the oil free emulsifiable concentrate is used at the rate of 2 liquid ounces per 100 bushels of seeds. The 2 liquid ounces of the undiluted material is added to the amount of water that is normally used for 100 bushels in that particular slurry machine. When the oil free material is used without a fungicide or other materials, it does not show on the grain and the left-over treated seeds may be fed safely to livestock. The addition of toxic fungicides to the slurry would prevent such a use.

Based on recommendations of the U.S. Department of Agriculture, this concentrate may be diluted with 29 volumes of a mixture containing equal amounts of odorless base oil and tetrachlorethylene, by weight, for use in thermal type generators like the Tifa and Swing Fog. It is used at the rate of 2½ pints per 10,000 cu. ft. of the space above storages of almonds, beans, cocoa beans, copra, cotton seed, flaxseed, grain sorghum, oats, peanuts, peas and walnuts for killing adult moths. These space treatments are applied at intervals of two weeks during the warm months of the year.

For treatment of bulk peanuts in the husk and based on a recommendation by the U.S. Department of Agriculture, one may use a dilution of the oil free concentrate 60-6 with 11 volumes of the mixture consisting of equal parts of tetrachloroethylene and odorless base oil, by weight, giving 5% piperonyl butoxide and 0.5% pyrethrins. It is applied at the rate of 2 gals. per 100,000 cu. ft. of nuts in such mechanical generators as the Microsol, Challenger, Skilblower, or as a finely divided spray. One pint is used per 10,000 cu. ft. of space above the load, or 2 gallons is applied in an average warehouse 100' x 100', with 15 to 20 feet of space above the load.

### SAFETY OF PIPERONYL BUTOXIDE AND PYRETHRINS

A recognized safety of pyrethrins has resulted from an aged and extensive use of pyrethrum dusts and sprays for control of insects in the household and garden. The frequently reported safety of these insecticidal materials was more fully understood when the previous beliefs were confirmed in acute and chronic feeding studies by Dr. A. J. Lehman. His findings were reported in 1951, *Bull. Assoc. Food and Drug Officials*, Vol. 15, p. 126, and in April 1952 in this Bulletin, Vol. 16, p. 48. It was found that the MLD 50 for pyrethrins in rats was 200 mg./kg., and that rats consuming 1000 ppm of pyrethrins in all their food in chronic feeding tests tolerated these amounts without any gross effects of injury to the animals. The lowest dietary level with gross effects was 5000 ppm, and this was the lowest level to show any damage of tissues. Dr. Lehman, *Bull. Assoc. Food and Drug Officials*, Vol. 18, p. 11, states that there is a rapid detoxification of pyrethrins and that rats can ingest more than an acutely fatal dose every day throughout their lifetime with little or no injury. This means that the safety of pyrethrins is well established by an authoritative source, and because of this feature, pyrethrins are remarkably well suited for the control of insects about foods.

The safety of piperonyl butoxide was first studied acutely by M. P. Sarles, W. E. Dove and D. H. Moore, who published their results in January 1949, *American Journal of Tropical Medicine*, Vol. 29, pp. 151-166. Following these studies, chronic feeding tests and other studies were made by M. P. Sarles and W. B. Vandegrift, and these were published in September 1952, *American Journal of Tropical Medicine and Hygiene*, Vol. 1, pp. 862-883.

In checking upon the safety of piperonyl butoxide, Dr. Lehman found that the oral MLD 50 in rats for piperonyl butoxide was 11,500 mg./kg. In the chronic feeding tests on rats, the lowest dietary concentration used and one that showed gross effects

upon the animals was 5000 parts of piperonyl butoxide per million parts of food. The same level showed some dosage of tissues which was of a reparable nature.

The studies by Lehman were greatly extended by Sarles and Vandegrift. The early evidence of the low toxicity of piperonyl butoxide to warm blood animals were followed by subacute toxicity tests, by graded dosage chronic toxicity tests on rats and dogs, a low dosage chronic test on goats, a short term experiment of low and moderate dosages on monkeys, and an extended use of sprays for four years on beef and lactating dairy cows.

1. In the laboratory tests there was a low order of toxicity which showed little difference in susceptibility between sexes or between species of animals.

2. The chronic feedings beginning at weaning time of rats and extending through three successive generations were conducted on food consumption, weight-gains of the animals and possible effects upon reproduction. In these studies there were no indications of any cumulative toxic effects in the second and third generations, even up to 10,000 ppm of piperonyl butoxide in all of the food consumed. The use of 1000 ppm alone, also this amount with one-sixth as much pyrethrins were tolerated equally as well by healthy animals.

3. In one-year graded dosage dog experiments, in which the animals were fed six times a week by capsule, the use of 3000 ppm of piperonyl butoxide was tolerated with only a moderate toxic effect.

4. At autopsy, histo-pathologic studies were made from microtome sections that were prepared from regular and special fixations, and by selective and general stains of the tissues of all organs of representative animals. These were made by Dr. William B. Vandegrift, an exceptionally well qualified outside pathologist who had a very special previous experience in the study of rat tissues. Based on studies made by Dr. Vandegrift, it was concluded that technical piperonyl butoxide is not carcinogenic for the liver. The studies also justify the conclusion that the compound did not exert a malignant tumorigenic effect upon the general tissues, nor upon the endocrine glands and breasts, and that it did not have an indirect general tumorigenic effect through disturbance of the endocrine glands.

5. Biochemical balance studies made on a dog indicated that large doses of piperonyl butoxide fed by stomach tube were quickly eliminated in the feces and only traces appeared in the urine. From separate feedings, 78 and 87.6% of the piperonyl butoxide were passed in the feces of the animals within 48 hours. This means that the material is poorly absorbed by the animal.

6. Cattle sprayed for control of flies and lice for four successive years, and also sprayed prior to and right up to the time that samples of meat and milk were obtained showed no piperonyl butoxide in the muscle, fat tissues or milk.

7. Based upon the absence of any effects in Group IV of the second two year experiment with rats (Sarles and Vandegrift), and allowing for a 100-fold safety factor, there is conservatively a safe human tolerance for 42 parts piperonyl butoxide and 7 parts pyrethrins per million parts of food, even when these amounts are present in all foods that are consumed.

#### RESIDUES REMAINING ON GRAINS AND IN MILLED FRACTIONS

Using a colorimetric method for detecting piperonyl butoxide (Jones *et al.*, Jour. A.O.A.C., Vol. 35, pp. 771-780), analyses were made of samples of different storages of wheat, corn and other grains at intervals throughout the periods of storage. The greater stability of piperonyl butoxide above that of pyrethrins, even when used together, readily suggested that one needs to consider only the butoxide present as an index to the presence of both materials. For both sprays and dusts, the bases have definite ratios which are never less than 1 to 10. This method of analysis for piperonyl butoxide was found suitable for whole grains, ground grains, wheat germ and wheat flour, when precautions were used for preventing interfering materials. As examples, on whole grains 88% of the piperonyl butoxide was recovered from laboratory treated



wheat, and 93% was recovered from similar samples of corn. Even better recoveries were obtained from ground grain and wheat germ. From wheat flour, there was an 80% recovery from samples treated at 2.5 ppm, 85% at 5 ppm, and 92% at 10 ppm. Final color readings on duplicate extractions of a single sample usually show less than 5% difference between minimum and maximum values. Freshly treated samples are always included for showing the efficiency of the analytical method.

The scope of the present paper does not permit a report on the detailed results with different grains. In all lots of stored wheat, corn and other grains, the content of piperonyl butoxide declined consistently during a storage period of one year. After milling, as would be expected, the majority of the piperonyl butoxide appeared in the initial fractions of screenings and scourings. Some was found in the wheat germ fractions of samples milled after 6 to 7 months storage, but none was detected in these fractions after the wheat had been stored for one year. No piperonyl butoxide was found in flour.

Three corn storages in Georgia and Maryland were treated with the protectant powder mentioned above to give theoretical initial residues of 14.3 ppm of technical piperonyl butoxide. These showed 7 ppm after 4 months, 6.5 ppm after 9 months, 6 ppm after 10 months, and 2 ppm after 15 months of storage. Milled fractions of portions of the corn at 8, 12 and 15 months after storage showed no piperonyl butoxide in the grits, meal, flour, germ or bran.

In Missouri, two storages of corn, 3300 bushels each, were treated with protectant powder to give a theoretical initial deposit of 29.5 ppm of technical piperonyl butoxide. Eighteen samples from each of these bins, taken 18 months after treatment averaged 5.6 ppm and 5.2 ppm, respectively.

In Kansas, two storages of corn, 3300 bushels each, were treated with oil free emulsifiable spray diluted as mentioned above, at the rate of 4 gals. per 1000 bushels, which gave a theoretical initial deposit of 12.2 ppm of technical piperonyl butoxide. Milled lots at 8 months after storage showed no piperonyl butoxide in grits, flour, or hominy feed. Each milled lot showed 1 ppm of the compound in meal, a grain fraction that accounted for 25% and 24% of the weight of the whole corn. In one of these, the corn germ represented 15% of the whole corn and showed 16 ppm. In the other, the germ represented 17.9% of the whole corn and showed 11.5 ppm of piperonyl butoxide. Calculations made from the analyses of all of these fractions showed the presence of 2.6 ppm and 3.5 ppm for the two lots of whole corn. Undoubtedly some of the piperonyl butoxide was lost by handling and tempering of the grain just before it was milled. Water is added to temper the grain just before milling.

These residue results illustrate the removal of, or reduction in, residual piperonyl butoxide in storage and in the milling process. They are representative of other studies made on other stored grains.

## CONCERNING THEORETICAL INITIAL RESIDUES FOR OTHER COMMODITIES

The residues that remain on bulk nuts, peas and similar commodities from the use of space treatments with piperonyl butoxide and pyrethrins are illustrated in the results of treatments of bulk peanuts (ground nuts) in the husk. On the basis of use of the recommended amount of 2 gals. of spray containing 5.0% piperonyl butoxide and 0.5% pyrethrins per 100,000 cu. ft. and assuming that all of the droplets entered the edible nuts, there would be a theoretical initial deposit of 0.466 ppm. Such a residue, even if it accumulated from repeated applications would permit 17 treatments during a season, without exceeding a tolerance of 8 ppm of piperonyl butoxide.

Sacks of grains, beans, peas, copra, cocoa beans and similar commodities that may be exposed to infested warehouses or in the holds of ships may need a surface treatment on the bags to protect them from infestations. A spray containing 3% piperonyl butoxide and 0.3% pyrethrins applied at the rate of 1 ml. per square foot of the surface of the sack would receive 10 ml. on 10 square feet of sack material. If it is assumed that all of the ingredients entered the edible portions weighing 100 lbs., there would be an initial calculated residue of 6.6 ppm, which is well within a tolerance of 8 ppm of piperonyl butoxide.

At canneries for fruit flies, space treatments with solutions containing 10% piperonyl butoxide and 1% pyrethrins are often used in mechanical aerosols at one ounce per 1000 cu. ft. of space. If we assume that all of the active ingredients of these treatments entered fruits having a diameter of  $2\frac{1}{2}$  inches, there would be a calculated initial residue of 1.55 ppm piperonyl butoxide. If a contact spray is used that contains 0.1% piperonyl butoxide and 0.01% pyrethrins, at 6 pints per van load of 4000 lbs. of fruits, there would be a calculated initial residue of 1.5 ppm of piperonyl butoxide. For either use it is inconceivable that repeat treatments would exceed the allowed tolerance of 8 ppm.

In the field where fruits and tomatoes are harvested, it is permissible to dip cracked open tomatoes or injured fruits in a suitable emulsion containing 1% piperonyl butoxide and 0.1% pyrethrins. Tomatoes, pears and fruits of similar sizes would have a calculated initial residue of about 7.5 ppm piperonyl butoxide. This is sufficient to prevent egg laying of fruit flies for about 48 hours or longer. One-half the concentration of the same ingredients is effective for about 24 hours.

### OFFICIAL TOLERANCES

The Food and Drug Administration, Department of Health, Education and Welfare, Washington 25, D.C. published under Title 21 Food and Drugs in the *Federal Register* dated March 11, 1955 an order on tolerances and exemptions from tolerances for pesticide chemicals in or on raw agricultural commodities. These were based on findings of fact as developed on public hearings held in 1950, and did not take into account technical and research advances made since that time. It stated as used in agriculture today that no tolerances need be established for the residues of pyrethrins, pyrethrum or piperonyl butoxide (piperonyl cyclonene and rotenone also were included) under Section 406 of the Federal Food, Drug and Cosmetic Act. It added that these materials should be exempted under Section 408 from the requirement of a tolerance when applied to growing crops. These proposed exemptions became effective 90 days after the date of publication.

Under Title 21 — Food and Drugs — the Food and Drug Administration added two new sections which were made effective upon publication in the *Federal Register* of February 15, 1956. Sections numbered 120.127 and 120.128 provided for tolerances of 20 ppm for residues of piperonyl butoxide and 3 ppm for residues of pyrethrins following post harvest uses on barley, buckwheat, corn (including popcorn), rice, rye and wheat.

Following further certification by the U.S. Department of Agriculture on the usefulness of the materials for post harvest applications, the Food and Drug Administration published its most recent order in the *Federal Register* of August 9, 1956. This provided a second paragraph to sections 120.127 and 120.128 and authorized tolerances of 8 parts piperonyl butoxide (butyl carbityl) (6-propyl piperonyl) (ether) and 1 part pyrethrins from post harvest use in or on the following raw agricultural commodities: almonds, apples, beans, blackberries, blueberries, (huckleberries), boysenberries, cherries, cocoa beans, copra, cotton seed, crab-apples, currants, dewberries, figs, flaxseed, gooseberries, grain sorghum, grapes, guavas, loganberries, mangoes, muskmelons, oats, oranges, peaches, peanuts, pears, peas, pineapples, plums (fresh prunes), raspberries, tomatoes and walnuts.

These tolerances and the impressive list of commodities to which they apply represent the first official clearances for post harvest uses of a pesticide in the United States. They show that insecticides made of pyrethrins and piperonyl butoxide fully comply with health standards and the provisions of the new pesticide law known as the Miller Bill. This is assurance to producers and handlers of grains who seek continuing markets, and to consumers who do not wish to compromise on the health or safety of their own folks.

In the past, some grain storages in foreign lands have made use of pesticides of doubtful safety. This was done as a risk, rather than suffer the usual losses from insect damage. Such a doubtful or hazardous health procedure is no longer necessary.

Pyrethrum and piperonyl butoxide are generally available in different parts of the world and may be obtained at reasonable costs from different sources of supply.

Buyers in foreign countries are no longer obliged to purchase grains that have been treated with materials of doubtful value or safety. They are now able (1) to specify and get grain that has been treated with pyrethrins and piperonyl butoxide, (2) buy untreated grain with the provision that it be treated with these materials as the grain is loaded, or (3) they may obtain either the power or liquid protectants that contain these materials and have them applied as the grains are being handled or stored.

As a last word, it may be said that there is little excuse for the use of materials that are or may be dangerous if safer materials are available to accomplish the same purposes.

### DISCUSSION

E. A. PARKIN. Have you experimental data on the loss, if any, of pyrethrins and piperonyl butoxide on passage through the Swingfog or Tifa machines?

W. E. DOVE. In the early work at Orlando it was determined that pyrethrum extracts would not be affected by the heat of fog generators because it was injected into the fog stream after it left the generator. Pyrethrins do withstand high temperatures in paper coatings which are applied during a split second exposure.



# Protectants for Farm Stored Grain<sup>1</sup>

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## ABSTRACT

*Grain protectants of various formulations which include pyrethrins synergized by piperonyl butoxide were applied to approximately 40 million bushels of wheat during 1955. Extensive tests with these products in the laboratory and in farm storage have been in progress at Kansas State College since early 1950. Approximately 450,000 bushels of grain, stored in 730 bins on 225 farms, were tested. Fourteen protectant formulations of liquids and powders were used in farm stored grain. Additional harvested grain before it was binned. With few exceptions, cooperators approved the formulations were used in the laboratory. Wooden granaries were selected for test purposes since generally they are more unsanitary and therefore provide the most rigorous conditions.*

*In all farm tests, the protectants were applied by farmer cooperators to newly protectant program and found the procedures for applying both powders and liquids simple to understand and easy to use.*

*The tests demonstrated that protectants were effective in preventing development of most grain-damaging insects during the first storage season when used in liquid or powdered formulations and applied at dosages and in the manner recommended by the manufacturers. Even at low dosages, grain-damaging insects were appreciably less abundant in treated than in untreated grain. Grain stored under especially unsanitary storage conditions, as in animal shelters or with feed grains and ground feeds, required higher dosages than grain stored under more sanitary conditions.*

Grain protectants consist of formulations of chemicals having toxic and repellent action, or both, for grain-damaging insects. Generally they are applied to prevent infestation but they may be applied to destroy existing infestations. In the United States, grain protectants must meet the toxicity claims stated on the label and must fulfill the safety and adulteration requirements established by the Food and Drug Administration under the Food, Drug, and Cosmetic Act. In addition they must not cause degrading of grain by imparting undesirable feel, odor, or other characteristics to the grain. For consumer acceptance, grain protectants must be easy to apply, must not adversely affect the grain for use as seed or feed, and must be cost-competitive with other insect control measures. Grain protectants now fulfilling these requirements and having both toxic and repellent action consist of formulations of pyrethrins synergized by piperonyl butoxide for application as sprays or powders. An estimated 30 to 40 million bushels of grain, largely wheat in commercial storage, were treated with these grain protectants during 1955.

Recent activities by inspectors of the Food and Drug Administration and demands by wheat buyers representing flour mills have stimulated interest in clean wheat at the farm level. According to the Monthly Kansas Crop Reports, there was an average of 100 million bushels of wheat and oats in storage on Kansas farms on October 1, 1953, 1954, and 1955. In addition, corn, sorghums, and other small grains raised this total to 150 million bushels, all of which was subject to damage by grain-infesting insects.

Much of the wheat stored on the farms was emergency storage, rather than a part of a regular, planned, grain storage program. The emergencies included shortage in elevator or boxcar space at harvest time, shortage of trucks or drivers, and income tax adjustments. The significant point is that many farmers stored wheat on their farms because they had no choice and they hoped that in future years it would go directly from the combines to the commercial elevator. This situation discourages construction of adequate storage facilities and the practice of desirable measures for grain sanitation. Inevitably, it results in infestations and damage by insects unless preventive measures are taken. With a planned grain storage program, the preventive measures will include

<sup>1</sup>Contribution No. 671, Department of Entomology, Kansas Agricultural Experimental Station.



“good housekeeping” and other management practices as primary steps and will depend on insecticides as a last resort. Where on-the-farm storage is an emergency program, an insecticidal treatment of protectants or fumigants likely will be the only measure used for insect control.

Emergency grain storage facilities on Kansas farms frequently have been decidedly unsatisfactory with respect to sanitation. Bins have been in all stages of disrepair; litter of spilled grain and feedstuffs have been scattered about the farmstead; market grains have been stored adjacent to infested feed grains; and animal shelters have been used as granaries.

The effective use of fumigants requires tight, well-constructed bins and a standard of sanitation sufficient that reinfestation will not immediately follow treatment. Competent observers have estimated that less than 20 percent of fumigations of grain in farm storage in the Kansas area results in satisfactory insect control because of: leaky bins; inadequate dosages; and improper application resulting from lack of knowledge or fear of the fumigants.

Tests conducted on Kansas farms during the past six years have demonstrated that protective sprays and powders containing pyrethrins synergized by piperonyl butoxide are admirably adapted for use under farm conditions. They will prevent insect damage for at least one season of storage under most circumstances. Approximately 730 bins of grain, largely wheat, on 222 farms were treated with seven formulations of protective powders and four formulations of protective sprays. To insure rigorous tests, wooden storage bins and sites rating from fair to poor in sanitation were selected for treatment. All applications were made by farmer cooperators with scarcely more than the instructions given on the label of the protectant containers. The powders were packaged in convenient sized sacks to assist in accurate applications; small hand trombone-type sprayers were supplied for applying the sprays.

The most successful formulation of protective powders contained 1.1 percent piperonyl butoxide and 0.08 percent pyrethrins impregnated in pulverized grain dust. It was applied at the rate of 75 pounds per 1000 bushels which deposited 13.7 ppm of butoxide and 0.99 ppm of pyrethrins.

The protective sprays were of two types. One was emulsifiable in water; the other was prepared for application with the pyrethrins and piperonyl butoxide dissolved in tetrachloroethylene as the carrier. The water emulsifiable formulations were applied in 4 or 5 gallons of water per 1000 bushels of wheat which left a residue of approximately 1.26 ppm of pyrethrins. The formulation with the fumigant carrier was applied at 2 gallons per 1000 bushels which left a residue of 1.12 ppm of pyrethrins.

The protectants were applied to uninfested wheat at some point between the combine and the bin, usually as the wheat poured out of the combine hopper into the truck bed, or as it was dumped from the truck into the lifter hopper. Without exception, farmer cooperators did not consider the application methods bothersome or impractical though a few objected to the dust resulting from application of the powders.

A prominent factor in practical tests with insecticides applied to grain in farm storage is the variability between the different granaries and within the same granary. The more significant of these variables include: availability of grain-infesting insects; size, shape, construction, and location of the bins; type and quantity of grain; thoroughness in application of the insecticide; dosage rate; moisture content and temperature of the grain; and the type of storage management practiced by the farmer. Because of the importance of these variable factors, it was thought inadvisable to compare one granary with another in determining results. Each granary had to be considered on its own merits without reference to other granaries. Also, in some instances there were no untreated check bins, since, during the latter part of the storage period, the presence of infested, untreated check grain influenced the rapidity of infestation of treated bins.

The procedures for evaluating results consisted of periodic sampling of all bins from harvest until November to determine the kinds and numbers of insects and the moisture content of the wheat. After November the results of the treatments were rated in terms of good, fair, or poor after taking into account the opportunities for infestation and assessing the probable damage without treatment. Bins with no infestation or with

light infestations in November were considered to have been protected from insects through June since the low winter temperatures would prevent insect migration.

The more significant conclusions drawn from these studies are as follows:

1. In general, protective sprays and powders containing pyrethrins synergized by piperonyl butoxide applied at recommended rates in an approved manner prevented damage to wheat and barley during at least the first season in farm storage.

2. The best results occurred when the protectants were applied as part of a grain sanitation program which included granary clean-up, application of residual bin sprays, and isolation of market grains from feed grains.

3. In some instances, standard dosages were not adequate when treated wheat of high moisture content was stored in particularly unsanitary granaries.

4. Even at low dosages, grain-damaging insects were more abundant in untreated than in treated wheat in the same granary.

Occasional unsatisfactory results in the Kansas area were found to be associated with inadequate dosage, improper application, particularly unsanitary conditions which provided a continuous source of infestation, and the presence of a few insect species such as *Plodia* moths which were not controlled by the single treatment at harvest time. In general, results were progressively more favorable from south to north in Kansas at the same application rates. This may be the result of more continuous opportunities for infestation, higher moisture conditions, and poorer storage sanitation found in Southeastern Kansas. Results with protectant treatments in Southeastern Kansas may improve with increased dosages, follow-up treatments, and improvement of sanitation measures.

Farmer cooperators have heartily approved the use of protective sprays and powders. Many have continued to use them and were instrumental in inducing their neighbors to do the same. But, in general, farmers have been slow in accepting the protectant treatments. This is explained in considerable measure by farmers' natural reluctance to spend money for a prevention treatment when, for so long, their thinking has been geared to control rather than preventive measures. However, as the clean grain program gains momentum and as increased pressures for clean grain are applied to farmers by elevator operators and other sources, the prevention treatment should gain favor rapidly. In fact, protective sprays and powders are the only insecticidal measures now available to protect much of the great volume of grain in emergency storage on the farm.

## DISCUSSION

C. J. R. JOHNSTON. What fumigants are recommended to farmers for treatment of their feed grain before harvesting of saleable grain?

D. A. WILBUR. We recommend any of the liquid grain fumigant formulations available on our market.

J. A. FREEMAN. To what extent do farmers in Kansas use grain protectants?

D. A. WILBUR. Kansas farmers have been slow in adopting the use of protectants.

R. W. HOWE. Some years ago a survey of farms in Britain showed that the common serious grain pests were never found in a granary kept entirely for the grain grown by the farmer himself. How far does separated storage restrict insects in the U.S.A. and do insects often fly into these granaries?

D. A. WILBUR. I do not have specific information on this point. However, I do not believe that flying insects nullify the effects of separation of market grains from feed grains.

M. H. BREESE. I would like to mention that a firm in Britain attempted to produce a polythene-lined bag in which grain would be protected from infestation from the outside and at the same time be hermetically sealed so that any insects present would deplete the oxygen and eventually die. Whether such a bag would be economically advantageous was not known. The use of bags was also contrary to bulk handling practices in the U.S.A.

D. A. WILBUR. There is a possibility of using such a container for seeds.

B. SMIT. Bags treated with pyrethrum for grain storage are being tested in South Africa with encouraging results.

D. A. WILBUR. Our grain is handled in bulk but there is a good possibility for using treated sacks for handling seeds.

E. A. PARKIN. If the farmer puts his sweepings in a drum, what measures would be recommended for quick and efficient treatment of this heavily infested material?

D. A. WILBUR. We would recommend that the farmer remove the sweepings from the granary to the feed room.

# Insect Damage to Southern Corn in Storage as Affected by Initial Field Infestation, Methods of Storage and Moisture Content

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## ABSTRACT

Corn grown in the South is subject to field infestation by the rice weevil. It is normally stored on the farm with the husk left in place, a condition that makes insect control difficult by insecticidal means.

Observations were made on insect damage to corn during storage of lots in which the initial field infestation was light, medium and heavy. Each lot of corn was stored as snapped corn, ear corn, field shelled, field shelled and cleaned, and shelled, cleaned and dried to 10 per cent. In a second series, corn at the 3 levels of field infestation was shelled, cleaned and dried to moisture levels ranging from 8 to 15 per cent.

After 6 months of storage, uniform samples were examined to determine the per cent kernels infested as well as insect abundance.

In series 1, insect damage was heavy in all lots where the corn was stored as snapped, ear or field shelled. Infestation and insect damage was less in the lots that were shelled, and cleaned, and least in the lots that were shelled, cleaned and dried to 10 per cent moisture. In all categories insect infestation and damage was greatest in the corn that had a heavy initial field infestation.

In series 2, there was a direct correlation between moisture content and insect damage. In corn with a light or medium field infestation, damage was light when stored at a moisture content of 8, 10 and 12 per cent. Corn with a heavy field infestation was severely damaged at moisture levels of 10 per cent or higher.

## INTRODUCTION

Corn grown in Southern Georgia is subject to field infestation by the rice weevil. The extent of infestation at harvest time varies from one field to another and may be influenced by the variety grown, the time of planting and harvest, and the proximity to sources of infestation. It is not unusual to find fields of corn having 60 percent of the ears infested at harvest time, with the average usually ranging from 25 to 30 percent.

In this region, it is the general custom to store corn in the husk, or as "snapped corn". The husk, if tight and long enough, protects the ear from infestation by the Angoumois grain moth and, to a certain extent, from other insects. However, in field-infested ears, it also protects the rice weevil from contact insecticides and renders fumigation impractical in many cases.

Logically, the extent of weevil damage to corn during farm storage should be dependent upon the degree of field infestation. To prove this point and to study the effect of moisture content and various methods of storage in relation to insect damage, the following experiment was undertaken.

## THE EXPERIMENT

Three fields of early planted corn (which were similar except for the intensity of rice weevil infestation) were selected near Alapaha, Georgia. All were hybrid varieties, grown on the same type of soil. Each yielded approximately 45 bushels per acre and was harvested during the last week in September with a comparatively low moisture content due to a prolonged dry period before harvest. One lot of corn from each field was harvested as snapped corn, while the remainder was harvested with picker-sheller.

The fields with the light and moderate weevil infestation were Dixie 18 hybrid, with an ear infestation of 11.0 percent and 26.6 percent, respectively, and a kernel

<sup>1</sup>This is one of the field stations of the Stored-Product Insects Section, Biological Sciences Branch, Marketing Research Division, Agricultural Marketing Service, U.S. Department of Agriculture.

TABLE I—Insect Abundance and Percentage of Ears Infested and Kernels Damaged in Corn with Light, Medium and Heavy Infestation at Harvest, after 6 Months Storage.

Degree of field infestation and manner in which corn was stored	Moisture content after			Insect infestation after 6 months storage		Live weevils per gallon sample after storage		
	Harvest	14 days storage	6 months storage	Ears infested	Kernels damaged	At breakdown	3 weeks later	Total
	Percent	Percent	Percent	Percent	Percent	Number	Number	Number
Light field infestation								
1. Snapped .....	17.89	17.70	13.97	31.4	17.0	23.3*	133.0	156.3
2. Ear .....	17.38	17.07	13.38	67.7	19.1	11.0*	148.0	159.0
3. Field shelled .....	17.78	17.43	14.30		10.5	101.0	32.0	133.0
4. Field shelled and cleaned .....	17.60	17.14	13.86		6.8	73.5	18.8	92.3
5. Shelled, cleaned, dried .....	9.88	10.07	11.05		1.2	1.8	0.0	1.8
Medium field infestation								
6. Snapped .....	19.53	19.07	14.22	43.6	27.6	30.0*	160.0	190.0
7. Ear .....	18.93	18.82	14.07	80.3	33.2	18.3*	142.5	160.8
8. Field shelled .....	19.22	18.82	14.13		17.9	121.8	28.2	150.0
9. Field shelled and cleaned .....	19.82	18.58	14.68		9.7	84.8	22.0	106.8
10. Shelled, cleaned, dried .....	9.92	10.05	11.07		2.3	2.3	0.7	3.0
Heavy field infestation								
11. Snapped .....	18.79	18.57	14.00	64.3	37.5	36.3*	273.3	309.5
12. Ear .....	18.27	17.27	13.56	83.1	40.8**	23.8*	239.5	263.3
13. Field shelled .....	19.02	18.65	14.28		29.5	208.0	45.0	253.0
14. Field shelled and cleaned .....	18.83	17.91	14.64		19.6	244.5	30.8	275.3
15. Shelled, cleaned, dried .....	9.88	9.94	11.97		13.4	56.8	7.7	64.5

\*When shelled for kernel examinations.  
\*\*Slight Angoumois grain moth infestation noted.



infestation of 0.70 and 2.1 percent, respectively. The heavily infested field was US-13 hybrid, with 37.6 percent of the ears infested and a kernel infestation of 4.8 percent.

In the first experiment, corn from the 3 fields was placed in 5 cubic foot bins constructed of masonite (pressed wood). It was stored as snapped corn (husk in place), ear corn (husk removed), field shelled, field shelled and cleaned, and field sheiled, cleaned and dried to a moisture level of 10 percent. Four replicate bins were prepared for each different treatment.

In the second experiment, corn from the 3 fields was shelled, cleaned, and separated into lots for drying to moisture levels of 8, 10, 12 and 15 percent. Four-bushel lots of each moisture level and the undried corn were placed in 5 cubic foot masonite bins. Four replicate bins were prepared for each moisture level.

All of the bins in both series were located in one large storage loft, and none of the bins was covered or otherwise protected from cross infestation. In addition, other infested corn was stored in the same loft, thus providing a source of rice weevils which could invade any of the bins at will.

At the end of 6 months' storage, the snapped and ear corn in the first experiment was examined for percent ear infestation and then shelled. All lots of shelled corn in experiment 1 and 2 were then examined for percent kernel damage and insect abundance. Insect infestation was determined by examining a 1000-kernel sample, and weevil abundance determined by screening a 1-gallon sample from each bin.

Since many of the weevils in the bins of snapped and ear corn were lost during the course of shelling and examination, insect abundance counts were again made of weevils in the gallon samples 3 weeks after the first count.

RESULTS

A summary of the data obtained in the examination of the corn is given in Table I for the first experiment and in Table II for the second experiment.

TABLE II—Insect Abundance and Percentage of Kernels Damaged in Corn with Light, Medium and Heavy Infestation at Harvest, after 6 Months Storage at Various Levels of Moisture Content.

Degree of field infestation and level of moisture content	Moisture content after			Kernels damaged or infested at end of storage	Live weevils per gallon sample
	Initial drying	14 days storage	6 months storage		
	Percent	Percent	Percent	Percent	Number
Light field infestation					
1. 8 percent .....	7.88	8.07	8.92	1.1	1.5
2. 10 percent .....	9.88	10.07	11.05	1.2	1.8
3. 12 percent .....	11.88	12.02	13.00	1.4	3.0
4. 15 percent .....	14.92	14.96	13.72	3.7	36.5
5. Field run .....	17.60	17.14	13.86	6.8	73.5
Medium field infestation					
6. 8 percent .....	7.86	8.06	8.98	2.3	4.0
7. 10 percent .....	9.92	10.05	11.07	2.3	2.3
8. 12 percent .....	11.90	12.08	13.69	7.1	42.8
9. 15 percent .....	14.90	14.97	13.71	10.4	99.3
10. Field run .....	19.82	18.58	14.68	9.7	84.8
Heavy field infestation					
11. 8 percent .....	7.94	8.06	9.02	5.2	5.3
12. 10 percent .....	9.88	9.94	11.97	13.4	56.8
13. 12 percent .....	11.84	12.00	13.97	15.2	98.0
14. 15 percent .....	14.73	15.04	14.34	18.0	211.0
15. Field run .....	18.83	17.91	14.64	19.6	244.5

From the data of Table I, it is evident that the initial field infestation has a direct bearing on the amount of weevil damage suffered by corn in farm storage during the first 6 months. Corn with a heavy initial infestation becomes more heavily infested and suffers greater damage than corn with a light field infestation. The greatest damage to the corn during storage was suffered by corn in the husk, in the ear, and field shelled but not cleaned. Cleaning the corn caused a marked reduction in both insect abundance and the percent of damaged kernels. By drying the corn to 10 percent, weevil populations and weevil damage were reduced to the vanishing point in corn from the fields with a light and medium infestation, and to a considerable degree in corn from the heavily infested field.

From the data of Table II, it can be seen that there is a direct correlation between the moisture content of stored shelled corn and insect damage. In corn with a light or medium field infestation, damage after 6 months of storage was light when stored at moisture levels of 8, 10 and 12 percent. As the moisture level increased above 12 percent, weevil damage increased in proportion. Corn with a heavy field infestation was severely damaged at moisture levels of 10 percent or higher. The corn from the heavily infested field was a variety more susceptible to weevil damage than that from the two other fields, so that it would be logical to expect a greater degree of damage under all conditions.

### DISCUSSION

V. M. KIRK. Were observations made on Angoumois moth damage in this experiment?

D. W. LA HUE. Very little damage was noted with any treatment, but no counts were made.

M. H. BREESE. Were the varieties grown tight-husked or were they the loose-husked hybrid varieties of the midwest?

D. W. LA HUE. Dixie-18 has a long, tight husk. U.S.-13 has short, loose husks.

# Developments in the Fumigation of Stored Products in the United States

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## ABSTRACT

*Developments in the field of fumigation of stored products in recent years have been concerned largely with improving the fumigation techniques for greater efficiency, economy, and the successful treatment of commodities in the many types of storage now used to conserve large surpluses of food products.*

*No outstanding new fumigants have been discovered since the advent of methyl bromide in 1931. However, by combining two or more chemicals, new and improved formulations have been developed.*

*The addition of ethylene dibromide or chloropicrin to methyl bromide enhances the value of methyl bromide for treating structures that are too loosely constructed for successful fumigation with methyl bromide alone.*

*The admixture of 10 per cent methyl bromide with carbon tetrachloride or combinations of carbon tetrachloride, carbon disulfide, or ethylene dichloride allows the great toxic properties of methyl bromide to be utilized in the fumigation of deep bulks of grain by surface application.*

*Forced circulation for the fumigation of bulk grain is an outstanding development in the technique of fumigation in the United States. First advocated in Germany and later adopted by the Swiss the method is proving to be of great value. Grain aeration systems installed in ships' holds, quonsets, storage tanks, grain elevators and other storages have been successfully adapted for the recirculation of fumigants and probe duct-systems for use in loaded railway boxcars, bins, and warehouses. The successful use of methyl bromide and other fumigants for the fumigation of bulk grain by this method has greatly reduced the cost of treatment and increased the efficiency of fumigation.*

*The use of gastight tarpaulins for fumigating stacked commodities, outdoors, in loosely constructed or oversize structures, or for wrapping entire bins or warehouses is another development of great interest and importance.*

*The success of any fumigation depends on maintaining a sufficient concentration of gas in all parts of the structure for an adequate exposure period. The development of the T/C gas analyzer has provided the commercial fumigator with a rapid and accurate means of determining the concentration of gas in a building or commodity throughout the exposure. If the concentration falls below the effective level gas can be added.*

## INTRODUCTION

Developments in the field of fumigation of stored products during recent years have been concerned largely with improvements in the technique of fumigation to meet the need for greater efficiency, greater economy, greater safety, and for the successful treatment of commodities in the many types of storages pressed into service for the conservation of large surpluses of food products in the United States.

During the past 25 years the most outstanding new fumigant is methyl bromide. This material has become widely used for the fumigation of sacked or packaged commodities where its ability to penetrate and its rapidity of aeration are of marked advantage. Acrylonitrile has come into some prominence in the fumigation field and in admixture with carbon tetrachloride 34 to 66 by volume is widely used for the fumigation of stored tobacco and manufactured tobacco products. It leaves no odor and aerates from the tobacco rapidly. It is also available in a 1 to 9 mixture with carbon tetrachloride as a fumigant for stored grain.

Ethylene dibromide, although not of recent discovery, has become popular for a number of purposes. It is used extensively as a component of grain fumigant mixtures.

<sup>1</sup>This is one of the Sections of the Biological Sciences Branch, Marketing Research Division, Agricultural Marketing Service.

The addition of 5 percent by volume of ethylene dibromide to these mixtures greatly improves the kill in the surface grain.

Many new formulations have been made by combining two or more chemicals. In many cases the combinations have resulted in increased usefulness of the fumigants.

Before the method of forced circulation of fumigants was developed to its present stage of perfection, attempts to use methyl bromide alone for the fumigation of bulk grain were not successful. This led to the development of various formulations containing 10 percent methyl bromide, in carbon tetrachloride, in the 1 to 4 mixture of carbon disulfide and carbon tetrachloride, and in the 3 to 1 mixture of ethylene dichloride and carbon tetrachloride. These formulations all gave excellent results in the treatment of wheat stored in elevator bins at a dosage of  $1\frac{1}{2}$  gallons per 1,000 bushels.

For treating grain in farm bins, mixtures of methyl bromide with ethylene dibromide were proposed. Two such mixtures were combinations of 70 percent ethylene dibromide with 30 percent methyl bromide, and 80 percent ethylene dibromide with 20 percent methyl bromide. These mixtures containing methyl bromide are not used extensively for the treatment of stored grain at the present time.

As space fumigants in warehouses 70-30 mixtures of methyl bromide with ethylene dibromide or chloropicrin were found to be useful for the treatment of warehouses that were not quite tight enough for methyl bromide alone.

The need for better sanitation in flour mills led to the more frequent use of local or spot fumigants with less dependence upon the general fumigation. In the past few years spot fumigants of comparatively low toxicity, such as the 3 to 1 mixture of ethylene dichloride and carbon tetrachloride, are being replaced by more toxic formulations such as the 70-30 mixture of ethylene dibromide and methyl bromide. The periodic use of these fumigants every 2 or 3 weeks enables the miller to hold insect populations at a low level throughout the year. Automatic applicators simplify the task of injecting small dosages at strategic points in the mill machinery.

### FORCED CIRCULATION OF FUMIGANTS

The forced circulation of fumigants through bulk commodities under atmospheric conditions was first described by workers in Germany (Meyer and Gliksman, 1932) and (Pustet, 1932). They successfully treated grain in elevator bins with methyl formate by circulating the fumigant through the grain mass by use of a mechanical aeration system. The method has been used in Switzerland and Germany for many years, but it was not until 1948 that it was tried out on a commercial scale in the United States (Phillips and Bodenstein, 1948). A year later its successful use in the treatment of cotton seed in metal storage tanks with methyl bromide was recorded (Phillips and Latta, 1949). Large-scale tests with the method for the fumigation of sorghum grain in oil-storage tanks were conducted in 1951 (Cotton and Walkden, 1951). In the ensuing 5 years the method has been widely adopted in this country for the treatment of bulk grain in elevators, farm bins, ships' holds, flat or warehouse storage, and in railroad boxcars.

The extensive employment of mechanical aeration and drying systems in grain storages encouraged experimental work to develop methods of adapting such systems for the forced circulation of fumigants. In describing experimental work with forced circulation of methyl bromide in bulk grain in ships' holds and grain elevators, Phillips (1955) concluded that, "(1) Rates of airflow comparable to those commonly used in grain-aerating systems promote satisfactory distribution of methyl bromide throughout bulk grain, (2) the recirculation method of applying methyl bromide can be utilized in silo-type grain elevators where the column of grain is 130 feet or more deep, or in flat bin storages similar to ships' holds, (3) fumigation can be completed within 25 hours and, (4) the fumigant remaining at the end of the treatment can be removed from the grain by the use of the system."

In general, the system consists of a floor duct or ducts, or a series of perforated lateral ducts radiating from a central floor duct, connected with a blower or blowers capable of pulling or forcing the fumigant through the grain with an airflow rate of approximately 0.1 cfm per bushel per minute, and a return duct or ducts from the blower to the overspace above the grain. The return duct can be located within the bin, warehouse or other structure, or on the outside. The pattern of the floor duct

system and the return duct system can be arranged to fit the situation. The fumigant can be circulated by pulling it down through the grain or by forcing it upwards through the grain.

In railroad boxcars loaded with bulk grain the system may consist of a series of metal tubes with perforated tips thrust vertically down through the grain to the floor and connected above the grain to a blower by means of a manifold. The fumigant released in the overspace is circulated by being pulled down through the grain and returned to the overspace through the metal tubes. The metal tubes can be connected individually with small blowers, thus eliminating the manifold duct. This latter arrangement is often employed to aid in the distribution of the fumigant through piles or bins of grain within buildings under fumigation in their entirety with methyl bromide, as in the case with khapra beetle eradication work.

The forced circulation method is not limited to any one fumigant, although more work has been done with methyl bromide than others. HCN has been successfully distributed in elevator tanks of wheat, and the distributing of heavier than air mixtures of carbon tetrachloride and ethylene dichloride, or carbon disulfide, have been accomplished experimentally.

### TARPAULIN FUMIGATION

The use of gastight tarpaulins for the fumigation of stacks of commodities, outdoors, in loosely constructed or oversize structures, or for wrapping entire bins or warehouses for fumigation has been another development in the fumigation field of great interest and importance.

Many types of materials are satisfactory for covering stacks for fumigation. The kind to be used will depend upon the type of fumigation for which it is intended and the material available. The least expensive type is an asphalt laminated fiber-reinforced kraft paper which can be obtained in rolls 6 to 8 feet wide and costing about 1 cent per square foot. The paper is fastened over a framework of wood constructed around the stack. This material is popular for covering stacks of trays of drying raisins in outdoor ranch storage, to destroy field infestations of the raisin moth. The edges of the paper strips are overlapped and battened down with strips of lath. At the base of the stack the paper strips are sealed to the ground with soil or with sand snakes.

In dry regions paper tarps are quite satisfactory for outdoor use and will protect the commodity from the weather, and to some extent from reinfestation from insects, for several weeks or months. Methyl bromide can be used successfully under this type of gastight sheet. Plastic tubes connected to one-pound cans or cylinders of the fumigant can be thrust through the paper walls to apply the fumigant. The holes can be sealed afterwards with plastic patches.

Other materials in common use for covering stacks for fumigation are: polyethylene sheeting, plastic-coated nylon, plastic-coated canvas, balloon cloth, rubberized fabrics, etc. Plastic-coated nylon tarpaulins are the sturdiest, but are high in cost. They vary in price from \$1.35 to \$3.50 per square yard depending upon their weight and whether one or both sides are coated.

Polyethylene sheeting, while less durable, is light to handle and inexpensive. A thin sheet of 3-mil gauge can be obtained for \$25 per 1,000 square feet. This material is used extensively to cover stacks of bagged rice in large, loosely constructed buildings. The covers are often left in place for the storage life of the stack so that they serve the double purpose of protecting the rice from dust, rain, and invading insects, as well as for fumigation with HCN or methyl bromide. When the sheets are to be used only for fumigation and are moved from one stack to another, a heavier sheet of 4-mil or even 6-mil gauge material is used. A polyethylene sheet 64 feet by 66 feet will cover a 4-carload stack of bagged rice.

The sheets are made gastight at the base of the stacks by the use of sand snakes. Fumigants are introduced by means of a plastic tube into an air dome formed by an appropriate arrangement of bags on top of the stack. If desired, the same conditions as required in a permanent fumigation chamber can be established in tarpaulin fumigation, i.e., load placed on a floor rack or pallet to permit circulation beneath it, a blower, and free access completely around the load.



In the fumigation of metal grain bins by forced circulation, the entire bin is sometimes covered with a tarpaulin. This serves to eliminate a return duct and avoids the necessity of sealing the ventilator and eaves of the bin.

In khapra beetle eradication work the difficult task of fumigating a building so as to kill all insects on the outside as well as the inside of the structure was solved by sheathing the entire building with tarpaulins. Some idea of the enormity of some of these operations can be gained when it is considered that the tarpaulins must enclose several million cubic feet of space. In one fumigation  $9\frac{1}{2}$  acres of plastic tarpaulins were required, together with  $10\frac{1}{2}$  tons of methyl bromide.

Standard, heavy, plasticized nylon tarpaulins are used over the roof and leading edges, with lighter skirts of polyethylene sheeting. The tarps are tightly sealed at connecting edges by rolling together about a foot of material of each tarpaulin and clamping with heavy duty, metal spring clamps. At the ground level the tarps are brought out about 3 feet from the building and the edges buried in a trench 12 inches deep, and covered with compacted, damp soil and sand.

For khapra beetle eradication a dosage of 5 pounds of methyl bromide per 1,000 cubic feet of space is introduced initially and circulated by means of fans placed at strategic points in the building. To aid in distributing the fumigant through piles or bins of grain within the building, individual gas recirculating units are inserted at various points in the grain mass. These units are made of 6-inch ducts leading to the floor level and are connected above the surface of the grain with neoprene hose to small blowers.

Gas-air samples are taken from many locations in the building during a 48-hour exposure period and if necessary, additional fumigant is introduced as needed to maintain a minimum gas concentration of 32 ounces of methyl bromide per 1,000 cubic feet for an aggregate of 24 hours out of the 48.

### PACKAGE FUMIGATION

The fumigation of individual packages of dried food products such as dried fruit, beans and peas, rice, soup stock, dog food, etc., has increased materially during the past decade, and has greatly reduced troubles from insect infestation in these products in trade channels.

Ethyl, methyl, and isopropyl formate are used extensively in the dried fruit trade, either alone or in combination with ethylene oxide, propylene oxide or other materials. The mixtures are intended to be both insecticidal and fungicidal in action.

For the package fumigation of dried food products other than dried fruit a number of fumigants have been found useful, including mixtures of carbon tetrachloride with acrylonitrile, ethylene dibromide, and methyl bromide.

Automatic dispensers are used that drop a measured amount of the fumigant in each package as it enters the sealing unit. They may be purchased as complete units or built from readily available parts to fit any situation. The installation should consist of the following: a tank of noncorroding metal to hold the supply of fumigant; a valve with a controlling mechanism such as a solenoid to automatically measure out the desired dosage, and a device to activate the valve such as a microswitch or a photoelectric cell. For careful measurement a timing device between the activating unit and the automatic valve may be useful. If there are fluctuations in the line voltage a voltage regulator is also desirable.

### USE OF THE T/C GAS ANALYZER

The success of any fumigation is dependent upon the maintenance of sufficient concentration of gas in all parts of the structure for an adequate exposure period. Chemical analysis of gas-air is somewhat cumbersome for commercial fumigation work. In European installations in grain elevators a gas concentration meter is used to control the flow of a 90-10 mixture of methyl bromide and carbon dioxide into the bins (Monro, 1952). The meter works on the principle of the thermal conductivity of carbon dioxide.

In the United States the recent development of the T/C gas analyzer for determining fumigant concentrations has provided the commercial fumigator with a useful portable unit for rapidly and accurately measuring gas concentrations during a fumi-

gation. The instrument used works on the principle of a resistance thermometer (Phillips and Bulger, 1953). A tungsten filament is heated by passing a known constant current through it. If a constant flow and ambient temperature are assumed, the filament temperature is a function of the thermal conductivity of the surrounding gas. When a new component is added which alters the thermal conductivity of the gas, electrical resistance is changed. This alteration in electrical resistance can be measured.

In practice, four filaments are placed in cavities comprising a conductivity cell. Two of these cavities contain a standard gas (air), and two are sampling cavities into which the gas mixture diffuses and bathes the filaments. The filaments are arranged in a Wheatstone bridge. The bridge is balanced at zero with dry air passing through the sampling line, and the moisture-free air containing the gas is pulled through at about 500 cc. per minute. The change in resistance creates an unbalanced circuit, and the resulting galvanometer deflection is a measure of gas concentration.

In actual practice, gas samples are taken from the structure under fumigation by means of previously installed plastic tubing. The conductivity of each gas sample is measured as it is drawn through the gas analyzer by a small suction pump. By calibrating the machine through comparison with chemical analysis, conversion tables have been made so that the galvanometer reading can be converted into ounces of fumigant per 1,000 cubic feet. The instrument has been calibrated for methyl bromide, ethylene dibromide, and mixtures of carbon tetrachloride with either ethylene dichloride, carbon disulfide, ethylene dibromide, or acrylonitrile. The vapors of the mixture can be measured only as a total of all components and these must be assumed to be in their original proportion. HCN is not easily measured by this instrument, but another unit is available for its measurement.

### USE OF HYDROCYANIC ACID TEST KIT

A simple test kit for determining concentrations of hydrocyanic acid in air has been devised by the manufacturers of hydrocyanic acid and is now available commercially.

It consists essentially of a 100 cc. syringe sampler so arranged as to draw a sample of the air to be analyzed through a scrubber containing a reagent. The gas-air sample bubbled through the reagent solution imparts a pink color to the solution which is matched with a permanent glass standards. A chart is available to determine the HCN concentration on the basis of the nearest matching color. The color comparator utilizes a special disk of ten different intensities of the pink color which forms when the test is carried out with the selected reagents.

After purging the gas sampling line the syringe sampler is attached with a piece of rubber tubing. Holding the sampler in the left hand, the left index finger is placed tightly against the opening at the bottom of the metal T-tube. The plunger of the syringe is pulled back at such a rate that 25 to 30 seconds are required for scrubbing 100 cc. of the gas-air mixture through the reagent. If a pink color does not develop with 100 cc. of air, the finger is removed from the T-tube, and the plunger pushed back to its original position to scrub another 100 cc. of air through the solution. On the other hand, if less than 100 cc. of air gives a satisfactory pink color that amount of air is sufficient for the test.

When a satisfactory pink color develops, the solution is transferred to one of the small tubes of the comparator and placed in the middle compartment. A small quantity of the test solution is poured into the other tube and placed in the compartment behind the color disk. The disk is rotated until the colors match and reference is made to the chart to obtain the concentration.

The color standards are based on scrubbing 100 cc. of gas-air mixture through 10 ml. of test solution. If 200 cc. of air are necessary before a satisfactory color develops, the HCN reading must be divided by 2, conversely if only 50 cc. of air are sufficient the reading must be doubled. The method of analysis is simple and direct for concentrations ranging from 5 to 5,000 ppm. This range includes the human threshold limit for industrial work room atmospheres as well as the higher concentrations which are encountered in closed spaces under fumigation. Portable kits complete with reagents are available at a cost of approximately \$100 per kit.

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## DISCUSSION

H. A. U. MONRO. The Chairman of this session, Dr. Parkin, has kindly permitted me to follow Dr. Cotton and to make a few remarks concerning the long-range program of the Fumigation Section of the London Science Service Laboratory dealing with the possibility of selecting strains of stored-product insects more resistant to halogenated hydrocarbon fumigants such as methyl bromide.

In a short note (*Can. Ent.* 88: 37-40, 1956) Monro and Uptis reported the isolation by selection of two populations of *Sitophilus granarius* (L.) more resistant to methyl bromide than the original stocks from which they were derived. The dosage of methyl bromide for 5 hours, exposure required for LD 50 of the selected adults was at that time approximately twice that for the non-selected controls. The mortality lines, plotted on logarithmic probability paper, were parallel. Since publication of the note four more selections have been made with only a small amount of increase in the dosage required for LD 50.

In a recent review Hoskins and Gordon (*Ann. Rev. Ent.* 1: 89, 1956) have differentiated between "vigor tolerance" and "true resistance" in the response of insects to selection by toxicants. In vigor tolerance the decrease in susceptibility is marked by the parallelism of the two log dosage-probit lines and by increased doses of comparatively low order. In true resistance, which may be due to the operation of biochemical reactions or possibly to morphological changes, there is initially a marked flattening of the ld-p line for the selected population with large increases in the doses required to produce mortalities.

From our results of three years of selection of the granary weevil by methyl bromide it appears that, so far, the only manifestation is the emergence of a type of vigor tolerance of a low order. Therefore, the outlook is good for the continued use of this, and possibly other halogenated hydrocarbon fumigants, against the granary weevil and other stored-product insects.

R. LATTA. I would like to place a question before the session as to the advantages of phosphine over calcium cyanide for the fumigation of grain.

B. SMIT. Phostoxin has been used in South Africa with very encouraging results.

E. A. PARKIN. Phostoxin is aluminum phosphide in tablet form which is introduced by a special spear into bulk grain or dropped on the conveyor. Reaction with grain moisture releases phosphine gas. There is no toxic residue after ventilation, especially if the grain is moved.

J. A. FREEMAN. Phostoxin has been used experimentally in the U.K. by the Pest Infestation Laboratory and the Ministry of Agriculture, Infestation Control. It has been used successfully even against heavily infested and heating sorghum. There is no dangerous residue.

H. A. U. MONRO. Has phosphine been tried in the United States?

R. T. COTTON. No, it has not been experimented with for the treatment of grain in the U.S.A. We have been quite interested in hearing of the excellent reports received recently from Australia regarding the use of this product for treating elevator grain.

# Tobacco Fumigants and Fumigation

By J. N. TENHET

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## ABSTRACT<sup>1</sup>

*Fumigation is the most effective means of controlling the cigarette beetle and is effective against the tobacco moth.*

*The three common forms of tobacco fumigation are: vacuum, atmospheric chamber, and space fumigation.*

*Vacuum fumigation is quick and highly effective, but expensive, and only relatively small quantities of tobacco can be fumigated at one time.*

*Atmospheric chamber fumigation is economical and reasonably effective, but slow and capacity is limited.*

*Space fumigation is less expensive and less effective; but large quantities of tobacco may be fumigated simultaneously.*

*The more commonly used tobacco fumigants are: hydrogen cyanide, methyl bromide, acrylonitrile-carbon tetrachloride 34-66, and ethylene oxide-carbon dioxide 1-9.*

*HCN is widely used for flue-cured tobacco. It is effective, but moderately expensive, and leaves a temporary odor on tobacco.*

*Methyl bromide can be used advantageously for cigarette tobaccos. It is not entirely safe for cigar tobaccos. It is effective and moderate in cost, but treacherous, and may injure cigar tobaccos.*

*Acrylonitrile-carbon tetrachloride is widely used for cigar tobaccos and Turkish tobaccos, and can be used for other types. It is easy to use, moderate in cost, and safe for tobacco. It leaves no odor on tobacco, but it dissolves rubber and corrodes iron.*

*Suggested dosages for tobacco fumigants are given. Recent research indicates the possibility of greatly increasing the effectiveness of space fumigation.*

## DISCUSSION

P. J. SPEAR. Please elaborate on the chemistry of bad odours resulting from methyl bromide fumigation.

J. N. TENHET. We have done no direct work on this. From other sources we have been informed that apparently a mercaptan is formed by the reaction of bromide with materials in the tobacco.

H. A. U. MONRO. Offensive odours have appeared in other commodities following methyl bromide fumigation when the products are mouldy. These odours appear to be due to reaction of methyl bromide with SH groups in the protein to produce mercaptans.

J. A. FREEMAN. Is it necessary to use elaborate fumigation methods to obtain deep penetration since infestation is usually confined more or less to the periphery of the package?

J. N. TENHET. Yes. Many infestations of *Lasioderma* penetrate 6 to 10 inches into the mass of tobacco in the hogsheads.

H. A. U. MONRO. Is the tobacco industry still satisfied that vacuum fumigation is sufficiently important to make further installations of equipment for this process?

J. N. TENHET. Yes.

C. J. R. JOHNSTON. 1. Do you recommend tarpaulin fumigation for hogsheads? 2. Do you inject fumigant into each hogshead? 3. What aerosol is recommended for space spraying?

J. N. TENHET. 1. Fumigation under tarpaulins is theoretically practical, but because of the type of warehouses in which tobacco is usually stored it is not economically feasible. 2. Fumigant is not injected into hogsheads of tobacco. 3. Use of aerosols is too large a subject to be discussed briefly.

<sup>1</sup>Published in *Tobacco* 144 (12): 22-26, March 22, 1957.

H. M. ARMITAGE. Does compression kill all insect life that might otherwise be present in bales? Also does not the subsequent entry of insects provide channels of entry for any fumigant?

J. N. TENHET. Compression kills few if any insects present in commercial bales or hogsheads of tobacco. The compression is not sufficient for that. Insect feeding tunnels through the compressed mass of tobacco probably do facilitate penetration of fumigants.



# The Khapra Beetle Suppression Program in the United States and Mexico

By H. M. ARMITAGE

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## ABSTRACT

Agricultural regulatory officials of Arizona, California, New Mexico and Mexico are co-operating under the direction of the United States Department of Agriculture in a sincere effort to eradicate all existing infestations of the Khapra beetle (*Trogoderma granarium*) within their respective borders. Following federally approved procedures an intensive effort is being made to locate all existing infestation; all infested premises are being fumigated in their entirety using five pounds of methyl bromide for each one thousand cubic feet of space held under gas tight covers, using measures assuring concentrations of two pounds per M/cf for any 24 hours, or one and one-half pounds per M/cf for any 36 hours, during a continuous 48 hour, or longer, period based on regular sampling of the gas concentrations at the most critical points during the full exposure period; also repeated spraying of the surface area adjacent to the structure under fumigation, out fifty feet, or to the nearest property line or natural barrier, which ever is the nearest, using five pounds of malathion, actual, in 100 gallons of diesel oil. Four hundred and four (404) premises representing approximately 120,500,000 cubic feet is involved to date, of which one-third in number and two-thirds in volume has been completed. Subsequent intensive survey has failed to show any survivals on any treated property and no new infestations have been recorded outside the quarantined infested area as originally defined.

The Khapra beetle (*Trogoderma granarium*) is one of fourteen species of *Trogoderma* found attacking stored grain and other agricultural seed in various parts of the world. It has long been known as a pest of rice in Japan, of barley in India, of wheat in Australia and the Philippines, of peanuts in Nigeria, and, more recently, of barley maltings in England. Laboratory tests have shown a wide range of grains and other seeds, particularly those of high protein content, to be highly susceptible to attack, not only as such, but also in milled or processed form.

It has been observed to increase under favorable conditions to almost astronomical numbers, the larvae often appearing to exceed in number the grain kernels making up the surface four or five feet of the infested grain mass. It is known to be a very dirty feeder, often damaging far more grain or seed than it consumes, resulting in losses that often run as high as 20% of the total storage.

Its increase in pest importance during recent years seems closely tied in with surplus production during and following World War II, with unusually extended, high volume storage, awaiting a favorable market, representing conditions inviting maximum infestation.

With this history it is not surprising that its appearance in Central California in November, 1953, not only for the first time in the United States, but for the first time in the western hemisphere, was viewed with considerable concern by growers, warehousemen, and processors, alike. Its finding also presented a serious problem requiring the attention of regulatory agricultural officials.

However, when first found, it seemed already too wide spread to permit any serious thought of attempting its eradication. Not only did a quick survey show it to be well distributed throughout the lower half of California, but also widely distributed in Arizona, with a few scattered infestations in New Mexico, and in Mexico just below the California border. For that reason the only immediate action taken was to inform handlers of grain and other agricultural seed of its importance as a storage pest and to suggest that they employ every available means to minimize further spread

from known infestations and, at the same time, make a concerted effort to hold the latter at as low a level as possible.

Serious thought of attempting eradication, however, was revived when a review of the meager world literature on this species, then available, showed that it had never been known to attack living plants and therefore field infestation not liable. Also, that while the adults had wings, they were apparently never used in extending their range. In other words, each individual infested premise might be considered as a separate unit and, given the means, such infestations could be progressively eliminated. Any possibility of further outward spread appeared restricted to carry-out of infested host material, or used containers, which could be prevented by the enforcement of rigid controls. The ultimate success of such a venture seemed limited only by the degree to which all existing infestation could be found, and by the degree to which further spread could be prevented in the interim.

Probably having the most at stake from the economic standpoint, the California Department of Agriculture decided to attempt the elimination of all infestations within its borders. Arizona and New Mexico authorities quickly followed suit. The United States Department of Agriculture was early convinced of the reasonableness and the desirability of such an effort and, in the interest of uniformity of action as between states, subsequently assumed responsibility for the direction of a well co-ordinated program, not only in the United States, but in co-operation with the agricultural authorities in Mexico.

Quarantine action was co-ordinated at both the state and federal levels, restricting the movement of all host grain or other agricultural seed from any infested premise to origin treatment, using measures developed concurrently by research workers in the University of California, and by federal workers in field laboratories established in California and Arizona. The effectiveness of these restrictive measures is demonstrated by the fact that to date, intensive survey has failed to record any extension of infestation outside the area originally defined, while any new infestations found within the latter area have been restricted to the finding and recording of those which must have been in existence at the time these restrictions were put into effect. It is true that a few new infestations involving on-farm storage did result from official permission, allowing grain and other agricultural seed to move from infested premises without prior treatment, where intended for immediate direct feeding or planting. Such action seemed economically expedient at the time. Actually the adverse results were minor and have not seriously expanded the suppression program.

The problem of eliminating infestation, even on a premise basis, has not been quite so simple. While there was considerable information available with respect to measures which might be expected to give satisfactory control, there was little or no information as to what measures might be used to secure eradication. Even the results of more recent research in this field did little more than indicate trends in effectiveness. Most of such work was done on the basis of LD-50 and LD-95, and occasionally at LD-99. However, the real problem lies in being able to obtain complete mortality of all stages in this remaining, very narrow, band of survivors, represented by the one to five percent, which can be expected to include those individuals or stages inclined to resistance.

The value of chemicals in planning an eradication program, applied as sprays or dusts, either in the presence or absence of host grain or seed, was quickly disproved. The habit of some larvae of secreting themselves deeply in almost imperceptible building crevices where they could not be reached by such measures, fully depreciated value of even the otherwise most effective contact or space insecticides, for this purpose. Also, the ability of such larvae to remain in hiding for unusually long periods without food—two to three years or even more—destroyed any practical residual value which chemicals applied in this manner might have.

In support of these conclusions an instance is cited in which the owner of an infested warehouse expended in excess of \$8000. in reducing larval infestation, after all host storage had been removed under quarantine safeguards, through alternate drenching applications, alone and in combination, of oil, DDT, parathion, malathion,

benzene hexachloride, and many others, to a point where no survivors could be found, only to have the newly introduced storage become more heavily infested than that originally housed.

Fumigation under gas-tight covers, using a highly penetrating fumigant, offered the only promising approach in meeting this problem. At the same time it presented a few new, and seemingly insurmountable obstacles to its use. For instance, the presence of larvae on the outside as well as inside of infested structures made it necessary that the latter be covered in their entirety, a field in which experience had been very limited, with the cost promising to be almost prohibitive. The situation has called for the covering, as a single unit, of mills and storage facilities up to 100 feet in height, connected by a maze of catwalks, conveyors, and ventilator assemblies running, in some instances, into millions of cubic feet.

Also, gas-tight covering has been found to be not only extremely costly but was not immediately available in the amount required. One unit later used the equivalent of approximately ten acres of plasticized nylon costing \$1.75 per square yard. Less expensive polyethylene sheeting has proved unequal to the wear and tear involved though, on occasion it has been used successfully as "skirts" when suspended from the heavier nylon. In many instances it has been necessary for commercial firms to pool their facilities in order to fully meet cover needs on a single job.

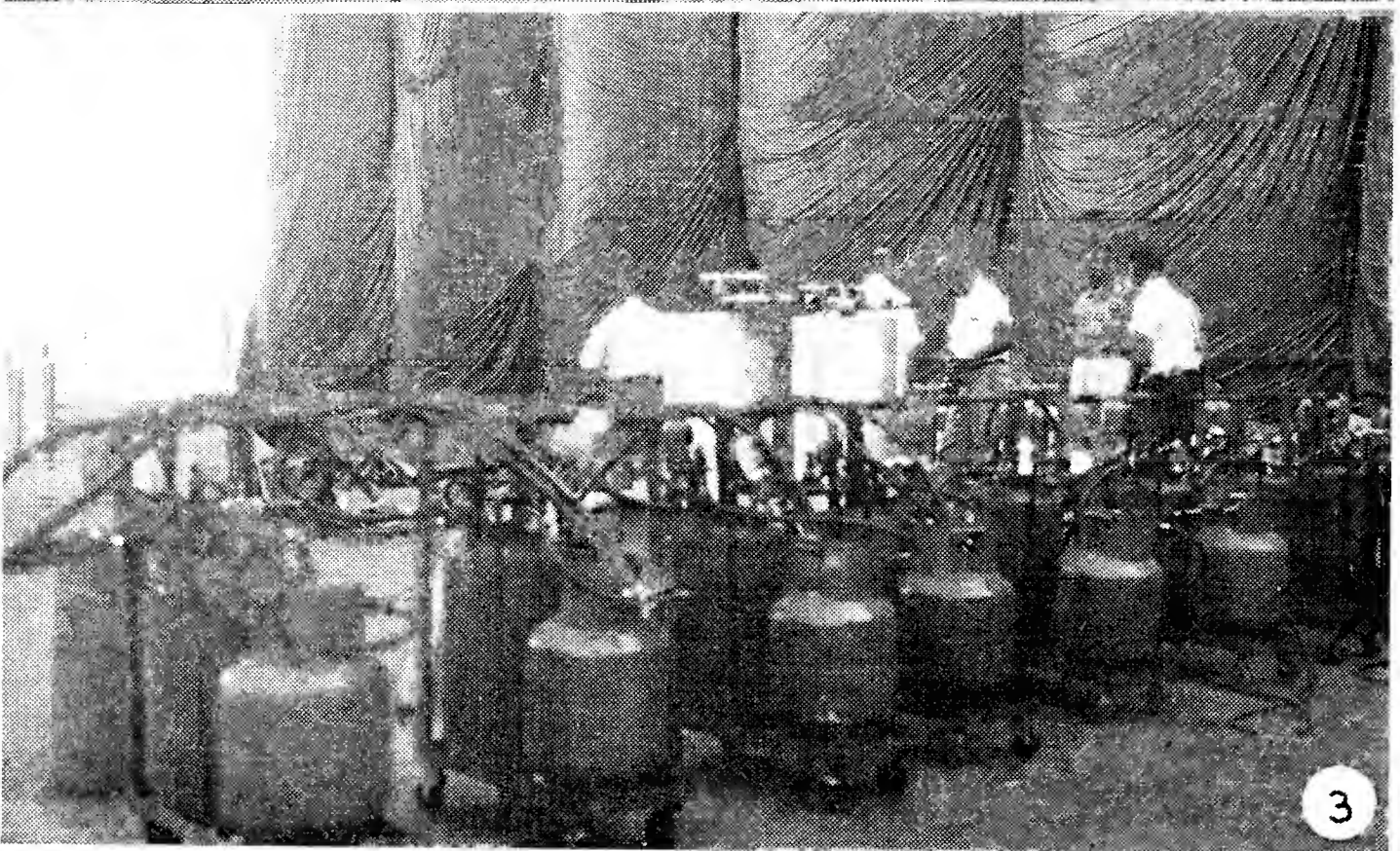
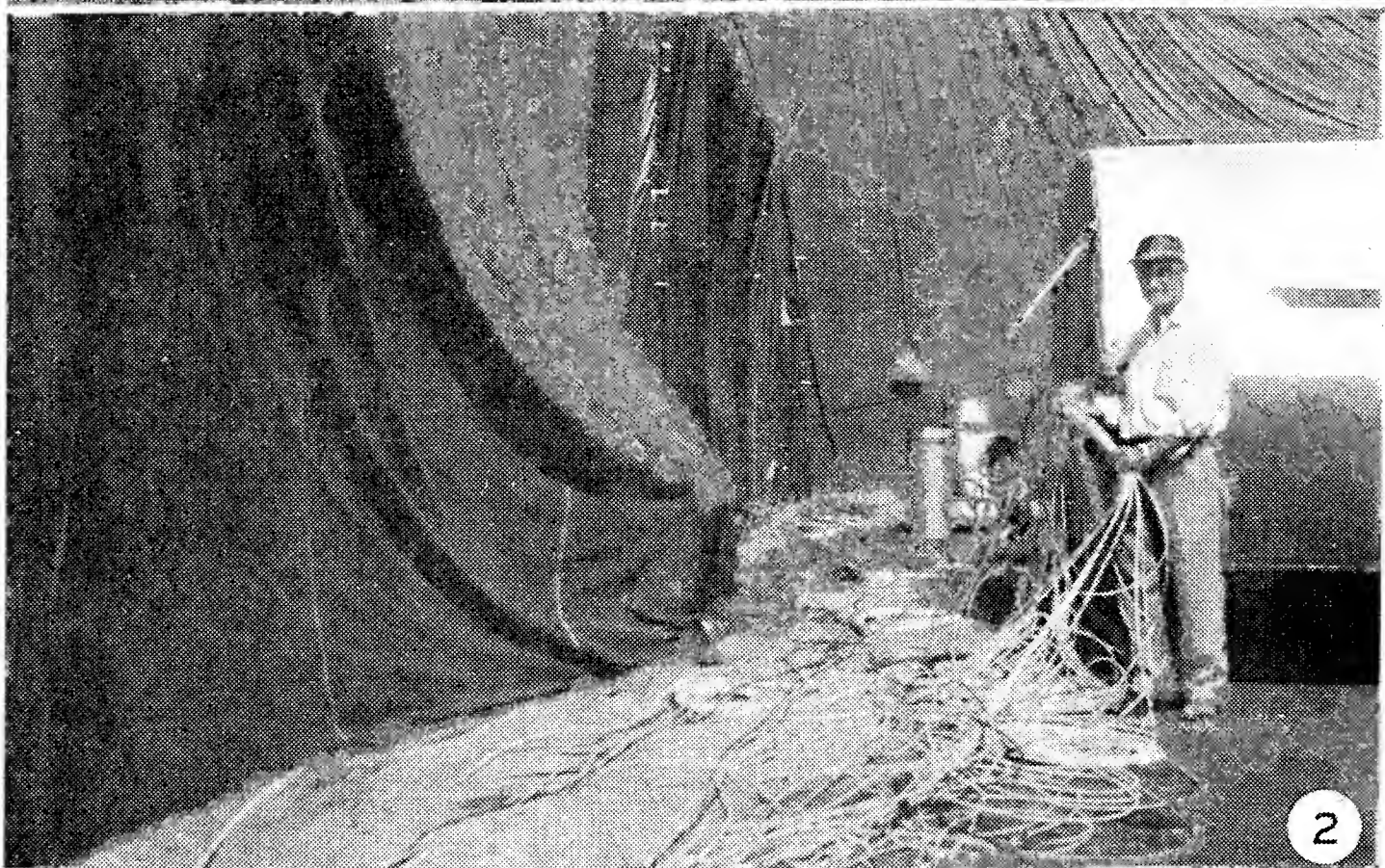
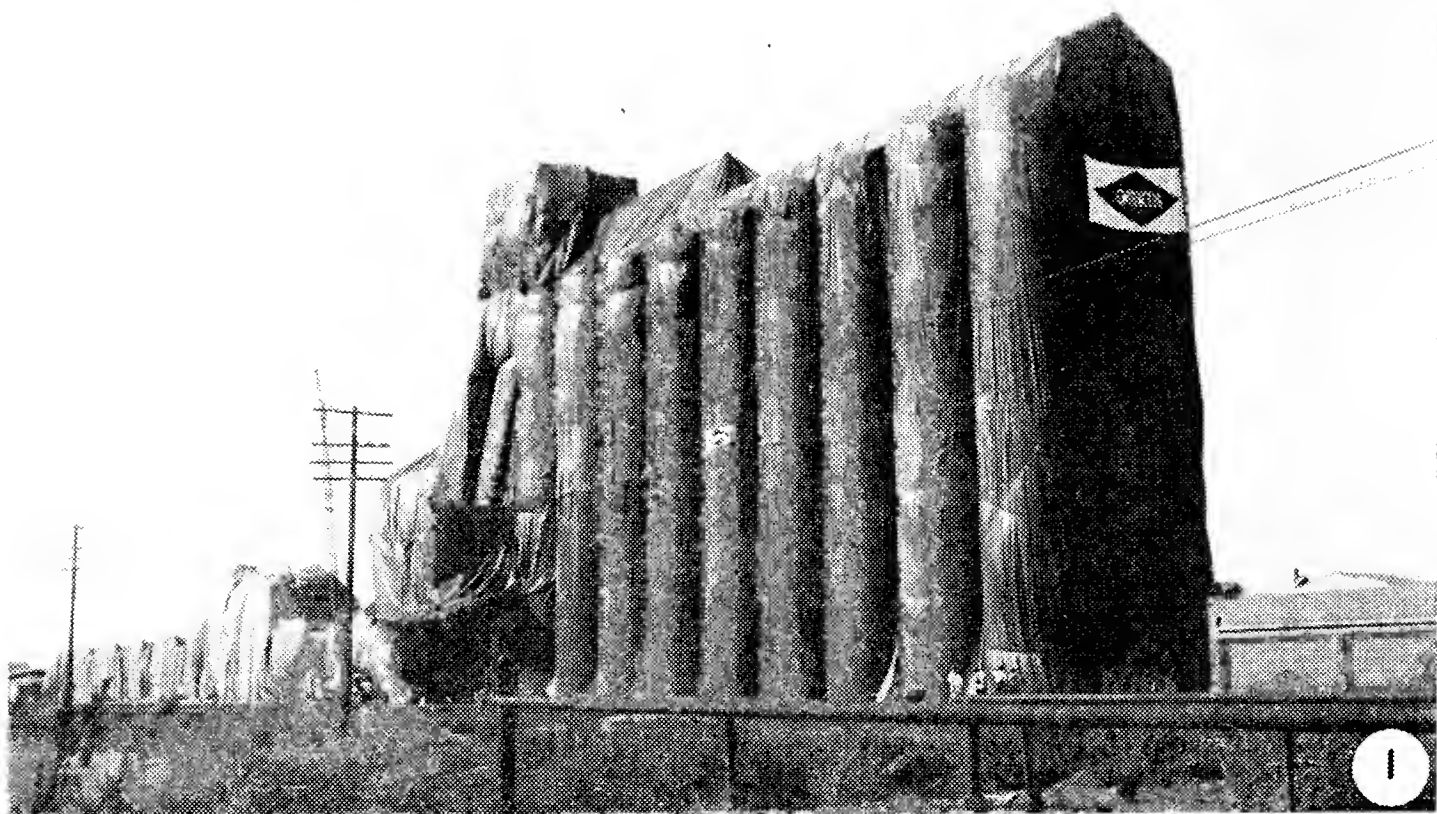
In selecting methyl-bromide as the fumigant to be used in this effort, it had already been proven effective against all stages of this species in meeting quarantine requirements where relatively small lots of host material were involved, using 3 to 4 pounds per M/cf for 12 hours. However, its history of poor dispersal in large grain masses, when used at similar dosages and exposure periods, was far from encouraging. Laboratory tests by University of California technicians had shown several other fumigants to be equally effective at lower dosages and shorter exposures. Nevertheless methyl-bromide was selected in the knowledge that it was non-explosive, non-inflammable, and less toxic to warm blooded animals than any of the others studied. These properties were exceedingly important in view of the high volume used on a single job, combined with the fact that the greater part of the work would be conducted in highly congested industrial areas.

It seemed reasonable to assume that the poor dispersal of methyl-bromide in grain masses, experienced by earlier workers, might properly be charged to the lower dosages and shorter exposure periods followed. Therefore, in order to be on the safe side, the use of 5 pounds per M/cf with an exposure period of 48 hours was adopted by the author, and later established as the standard in all future operations. This action stressed the importance of a longer exposure period though at the same time, stepping up the dosage appreciably over the formulations previously used. At the time it was thought that if this dosage and exposure period proved unnecessarily high, either or both could later be modified, downward. While later experience showed that such modification might be permissible within certain limits, the high investment in cover — \$47,500. in one instance — against the relatively low cost of the fumigant, suggested that such a move might be unwise. It was, therefore, deemed more practical to continue the original measures. At the indicated total cost, together with the serious disruption of commercial operations of the grain handlers during fumigation, it was obvious that few failures could be afforded.

But, before embarking on full scale operations, three rather large scale tests were arranged and carried out.

The first of these tests involved a simple type grain storage building comprising approximately 1,000,000 cubic feet which was devoid of any host storage. The conditions under which this test was conducted turned out to be such that they could not be readily duplicated. During the entire exposure period exceptionally heavy rain fell which gave practically a water-tight seal against gas loss. This situation was credited with the fact that the gas concentration curve never fell below 4 pounds per M/cf at any time during the 48 hour exposure period. In this test, thousands of larvae in controlled lots, were used as a check at all gas sampling stations, as well as at many other critical points throughout the structure. The complete mortality obtained under





these conditions was not unexpected but needed confirmation by other tests, under more normal conditions, to assure that this higher concentration was not mandatory.

In the second test another simple type grain storage warehouse was used, comprising 540,000 cubic feet, containing 3500 tons of heavily infested seed barley comprising a single mass measuring 300' by 50' with the grain leveled off at 16' in depth. Mechanical means of recirculating the fumigant through the grain mass was provided. Electric motor driven re-circulation units of 1000 cfm capacity against a 1" static pressure were installed in the grain mass, being spaced 24' apart in equidistant relationship to each other and 12' out from the sidewalls supporting the storage. These units were attached to 6" metal ducts penetrating the grain mass to within 2' of the floor. In operation they were supposed to draw the gas down through the grain and dispel it in the head-space above. These units were operated until complete equilibrium of the gas was reached both in the grain mass and in the open areas in the structure. This occurred at the end of 10 hours following introduction of the fumigant. Equilibrium was reached first at the floor level, then at the 8' depth in the grain and last at a point 30" below the surface of the grain. This suggested that the re-circulation units did not pull the gas down through the grain as expected. Rather, the results of sampling indicated that the gas was inclined to follow a normal flow down the side walls and out along the floor, gradually permeating upward through the grain mass, possibly speeded up by the re-circulation units. With the occasional addition of supplemental gas, equilibrium continued throughout the balance of the exposure period.

Need for supplemental gas was attributed to sorption in the loose, sandy soil under the structure. Concentrations of 27 ounces per M/cf were recorded 1' below the surface at the end of 48 hours. Four hours after the covering had been removed concentrations of 22, 40, and 10 ounces, respectively, were recovered at 8, 18, and 30" below the surface of the soil. This loss could possibly have been avoided by flooding the area before the gas was introduced but it was feared such action would protect hiding larvae and permit their survival. As in the first test, the examination of check specimens showed complete mortality of all stages at all locations.

The third test involved a more complicated structure of 740,000 cubic feet, including a mill, storage bins, and bulk storage. The latter was made up of 7500 tons of barley in a single mass 300' long by 50' wide and 12' deep at the sides with a maximum depth of 23' at the center as peaked throughout its length. In this instance no re-circulation equipment was used, the purpose of the test being to determine whether it was necessary. Without its use complete equilibrium of the gas throughout the grain mass and the structure was obtained in 15 hours, requiring only 5 hours longer than under re-circulation. However, this five hours could be extremely important in meeting the 48 hour coverage as later discussed. In the absence of re-circulation it was noted that the gas dispersal followed much the same pattern as in its presence excepting for the delay in reaching equilibrium. Following introduction into the head-space above the grain mass it appeared to slide down the slope of the peaked grain to the side walls and then rapidly down the walls to the floor. It then moved slowly outward along the floor, percolating upward through the grain mass with concentrations increasing progressively and the area just under the surface of the grain at the extreme peak, the last to come through. Again a check of test specimens showed complete mortality of all stages at all locations.

With respect to all tests as well as future operations provision was and has been made permitting the operation of 18" convection current electric fans, strategically placed, which were and are operated continuously during the full exposure period to assure circulation of the fumigant throughout the free space under the cover. Also

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← Fig. 1. Grain elevator, 1000' x 75' x 110' high (4,500,000 cu. ft.) with bins filled with bulk barley to depth 90'.

Fig. 2. Maze of 1/4" plastic tubing used to bring gas samples from pre-selected locations to thermal-electric gas analysers in central trailer laboratory to permit regular readings of gas concentrations.

Fig. 3. Battery of heaters used in introducing 10 tons methyl-bromide as a fully volatilized hot gas within a period of two hours.



with the exception of the first test all insect specimens used to check the effectiveness of the measures, originate on the premise under treatment. If the populations do not permit the collection of a sufficient number for this purpose complete reliance is placed on gas concentration readings.

The favorable results obtained with respect to all three tests seemed to confirm the effectiveness of the measures used and have been applied to all future operations. Those of the second test were particularly significant from the standpoint of eradication as the building used was the same as that in which the value of chemicals applied as sprays or dusts was disproven. For the second year following its fumigation this building has been used to store current harvest without detectable infestation being

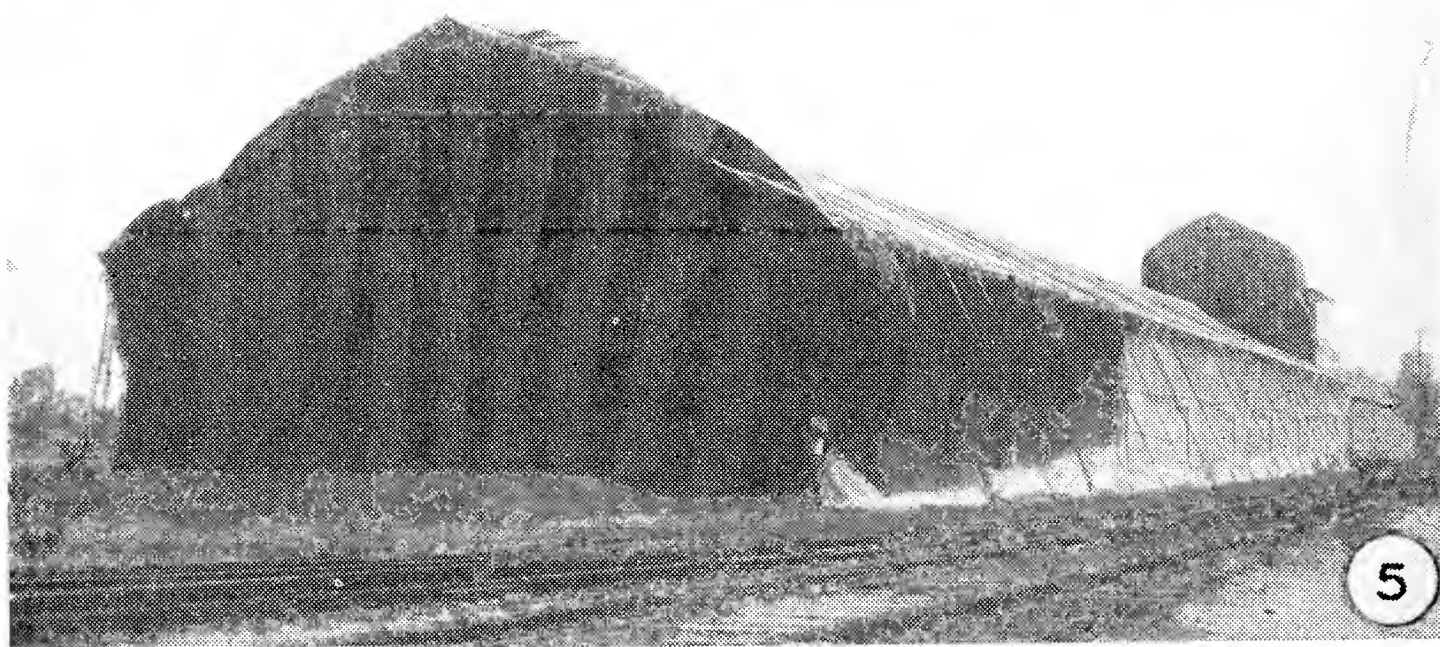
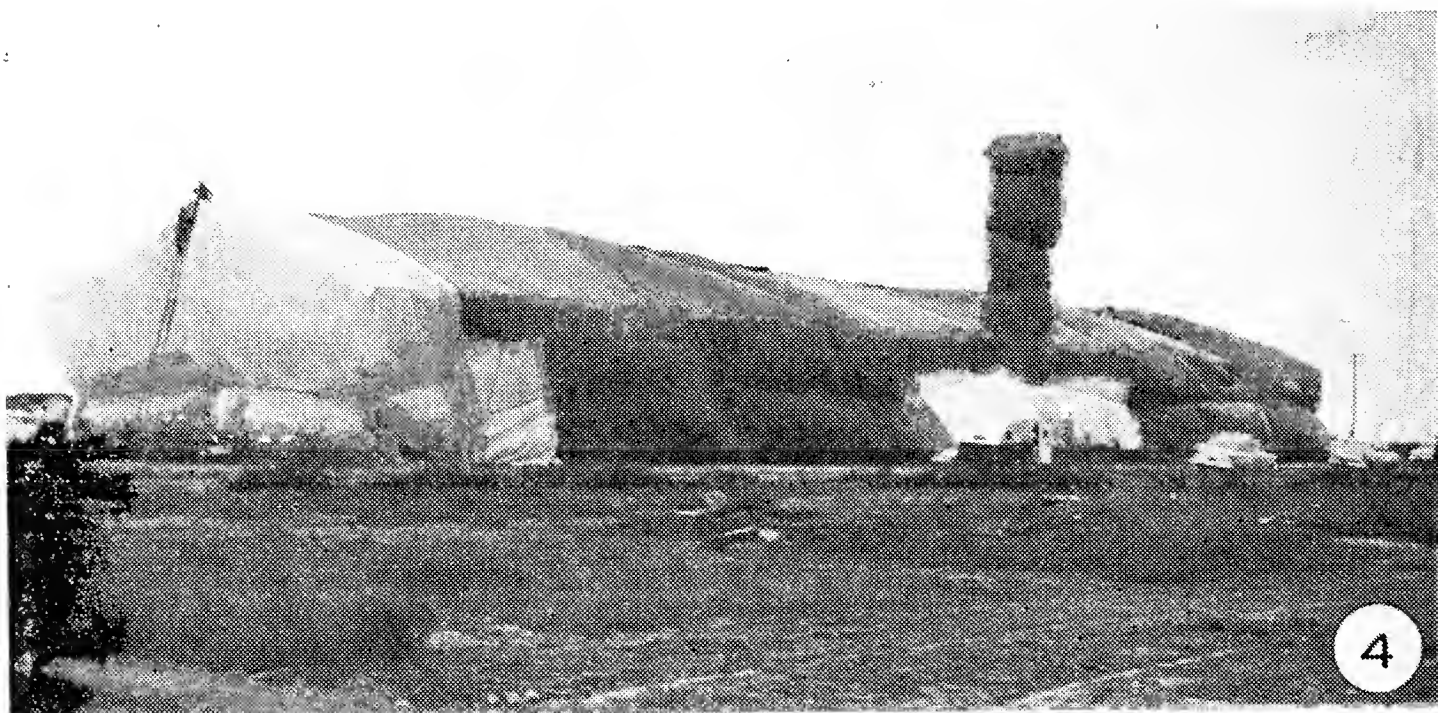


Fig. 4. This cover lost later due to windwhipping of balloons produced by surplus air accumulated during process of covering.

Fig. 5. This cover saved under similar conditions by removal of surplus air with 500° cfm. exhaust fan as soon as covering was completed.

found. The results reported have served as a sound basis for the current, all-out eradication program now being followed. However, in their application there are a number of pertinent details that seem to merit special mention.

For instance, in covering structures of this type for fumigation the tarpaulins are allowed to follow the contour of the building and its appurtenances to the ground with a loose draping effect so as to comprise a single unit. So called "package wrapping" or separate covering of conveyors and catwalks is discouraged as not being conducive to maintaining equilibrium of the gas in such areas. Often, however, such covering is necessary in order to avoid exposing too great an expanse of unsupported fabric surface to the wind. At the ground level the covering is brought out 3' and the edge

buried at least 12" deep in a trench filled with wet sand or even water, so as to obtain a good ground seal and thus minimize gas loss.

Obviously under such conditions the covering cannot be of a single piece but is made up of a number of standard fumigation tarpaulins the edges of which are rolled together with a lath between and so held with strong, metal, spring clamps. As many as 35,000 such clamps have been used on a single job.

The methyl-bromide is always introduced as a fully volatilized, hot gas, using heaters designed for that purpose. A maximum of two hours is allowed for the introduction of the gas regardless of how great the amount may be, the exposure period starting when its introduction has been completed. It may be introduced simultaneously from several outside pre-selected points. A hose or pipe, usually 2½" in diameter, is used to carry the gas to various parts of the structure so as to get good initial distribution. Such facilities are particularly important when attempting to fortify the concentrations in a certain part of a large structure, as introduction at a distant point would require too long a time in changing the concentration at the desired point. This is particularly true with respect to the head-space over storage bins.

Literally miles of ¼" plastic tubing is used in bringing gas samples to thermal-electric gas analyzers located at a central point close to the building under fumigation, usually a mobile trailer laboratory. From 6 to 50 gas sampling stations may be set up in advance, the number depending on the size and nature of the building. The direct readings made possible, representing gas concentrations, are usually checked against the chemical analysis of samples taken from representative locations. Readings are usually taken every two hours during the exposure period and watched carefully for any indication of a drop in concentration at any specific point. It has been found much easier to hold concentrations at the desired level by the timely introduction of supplemental gas than to try to bring them up after they have fallen too low.

One of the biggest problems encountered in fumigation operations on the scale required has been that of maintaining the cover intact for the full 48 hour exposure period. Daily afternoon or evening winds of intensities varying from 5 to 25 miles per hour are the rule rather than the exception throughout the treatment area. So called "Northerners", usually of three days duration, with gusts up to 50 miles per hour, also are not uncommon. In many areas strong "dust devils", or local whirl-winds, are a definite hazard. In view of the vast expanse of fabric exposed in covering the buildings, any of these winds can and have repeatedly played havoc with the cover resulting in total or partial loss of the fumigant. Tight as the clamps are that are used in holding the tarpaulins together, any excessive strain, particularly wind whipping, can break them loose.

Further aggravating the wind problem, considerable air is trapped during the process of covering. During the heat of the day this surplus air expands. Either results in the formation of huge air bubbles or balloons which aid wind-whipping with ultimate cover tear or loss of connecting clamps. This situation has been met by removing this excess air through the use of 5000 cfm exhaust fans, thus pulling the cover tight against the building. Care must be exercised to see that the cover is not pulled too tightly as in so doing clamps can be pulled loose and the precautions nullified. In the case of air accumulated during the course of making necessary cover repairs during fumigation, it has even been found possible to remove the air-gas mixture without interfering with the over-all concentration. Theoretically, the air remaining under the cover carries the same concentration as that removed. It remains only to introduce additional gas to compensate for that lost during the cover damage.

There is still another wind-cover problem. Even after being pulled tightly against the building the cover is subject to considerable wind-whipping due to the venturi action of the wind along the leading edges of the structure. This can only be partly prevented by stripping these edges in such a manner as to break the smooth flow of air. It is these continually recurring situations that make the 5 hours gained through the use of re-circulation equipment exceedingly important in assuring that the required gas concentrations for the required periods are obtained within the shortest possible time.

As a necessary supplement to the fumigation, careful attention is given to the surface area immediately adjacent to the building under fumigation. This area has been officially defined as that lying within 100', or to the property line or a natural barrier such as a road or irrigation ditch, which ever is nearest. Under population pressure larvae are forced outside an infested building and have been found in numbers as far out as 50' hiding under all types of ground debris, even a discarded match-book cover. Unless eliminated they could later find their way back into a fumigated building. As part of the approved eradication measures, it is required that all debris or accumulations in the area as defined first be moved or raked toward the building and included under the fumigation cover. The area is then sprayed twice at 24 hour intervals, immediately prior to the fumigation, using 5 pounds of malathion, actual, in 100 gallons of diesel oil, each time wetting the surface thoroughly. The area is harrowed or disced between each spraying. A third and final application is made immediately following introduction of the fumigant so as to overlap the two operations in the proper order. Where black-top paving is present water may be substituted for the oil as black-top and oil are not compatible. In these operations particular attention is paid to the area of receiving or loading out host material and to that used in the disposal of seed screenings.

Obviously, owners of infested premises have been exceedingly anxious that they be released from quarantine status at the earliest possible moment, not only to avoid the continued expense and inconvenience of treating all outgoing shipments, required as a condition of movement, but also to get out from under a virtual black-listing by uninfested receivers.

Not only did the Commodity Credit Corporation refuse to approve infested premises for government storage, thus cutting off a major source of revenue, but at one time the Grain Exchange even refused to quote prices on grain originating with infested premises. It was therefore early important that some specific yard-stick be established under which such release could be secured.

Based on the results of the tests cited, supported by further laboratory studies as well as field operations, the federal authorities have provided that any infested premise which has been subjected to over-all fumigation under gas-tight covering, using 5 pounds of methyl-bromide per M/cf, may be immediately released from infested status if it can be shown by supporting data that a concentration of 2 pounds for any 24 hours, or 1½ pounds for any 36 hours, during a continuous 48 hour exposure period, was maintained at all gas sampling stations. The supporting data required calls for the submission of gas concentration readings taken at 2, 4, 6, 12, 18, 24, and 48 hour intervals, representing not less than 6 carefully selected stations, including the most critical points in the structure, and in particular, the top, center, and bottom of any bin content or stacked sack material. Immediate release following fumigation is, of course, also subject to conformity with the approved measures dealing with the surface area adjacent to the structure under fumigation, as previously outlined. The entire operations must be conducted under official supervision.

When an infested premise does not lend itself to the type of fumigation outlined, any special approved measures may be followed and will be recognized if applied under official supervision. In such instances release is delayed for a minimum of one year, subject to negative findings based on intensive inspections made at 180, 90, and 90 day intervals, the final inspection to be made by the federal authorities who represent the controlling agency. Most of this type of situation has involved on-farm storage, or owners whose operations could not be satisfactorily separated from other activities in the same building such as banks, building and loan associations, and others, not amenable to being included in such measures.

The detection of all existing infestations is believed to be the keynote to the success of this effort. Visual inspection is not too effective in detecting light or incipient infestations requiring that potential host premises be inspected repeatedly at not less than thirty day intervals, with negative findings, before giving them a clean bill of health. Federal authorities have assumed this responsibility assisted by state and county personnel. Trained crews are riding out every road in the infested areas, stopping at every farm house and inspecting and recording for future reference, the loca-



tion of all potential host material. Carefully planned scouting surveys are being conducted in other than the infested states in cooperation with local state officials.

Surveys crews in the infested states are reported to be on the their fourth round of inspections. To date 51,000 premises in 27 states have been inspected of which 60% has been centered in the infested areas. The total number of infested premises recorded as a result of these inspections is 419 of which 272 are in California, 107 in Arizona, 5 in New Mexico, and 35 in Mexico just below the California-Arizona Border. These infested premises represent a total of 114,418,132 cubic feet to be treated. Already treatment has been completed with respect to 266 premises representing 63% of the total number, comprising 85,525,952 cubic feet which represents 74% of the total volume. These treated premises have been released from infested status. 153 premises comprising 28,892,180 cubic feet remain to be treated over half of which is now out to contract. It is reported that all currently recorded infestations will have been fumigated by the close of this year.

Co-related with this encouraging progress being made in treating infested premises, survey activities show that during June of this year 60 man-months devoted to the inspection of 2230 potential host properties in the three infested states recorded only 6 new infestations — 5 in Arizona and 1 in California. These 6 new infestations comprise less than 200,000 cubic feet. It is further encouraging that so far, intensive inspection has recorded no recurrence of infestation in any of the premises so far treated.

The sequence of operations in the eradication program has been to first treat those infested premises actively involved in the movement of host materials as representing the most immediate hazard of outward spread. On-farm storage for on-farm use has been the last to receive attention as there is no movement of host material from such premises. Used sacks are recognized as a possible means of spread from this type of premise and for that reason handled under rigid quarantine controls. Practically all known infested premises yet to be treated are of this latter type.

The manner of financing these operations has been varied to meet local conditions. In California the State Department of Agriculture originally bore the entire cost out of the state General Fund, as it has in many similar situations. Later when the United States Department of Agriculture entered the picture the latter assumed one-third of the cost, supplied in the form of chemicals and survey personnel. In Arizona the cost has been split three ways between the federal government, the State, and the property owner. In New Mexico the owners of the few infestations found in that state bore the entire cost with some federal aid. In Mexico the program is identical with that being conducted in the United States with the United States making appreciable contributions in money and personnel. In terms of dollars and cents the total cost of the program to date has been \$1,340,360. Of this total \$363,523. has been federal money, \$879,696. has been provided by the three infested states, and \$97,336. has been covered by owners of the infested premises treated or by representatives of the grain storage interests in those states.

In justification of this eradication effort from the economic standpoint, official records show that the 1955 national farm value of the major Khapra beetle hosts that are being protected was \$8,250,702,290. That of the three infested states during the same period was \$318,651,519. of which California, alone, accounted for \$263,796,675. If the Khapra beetle was accepted as an established pest and became widely distributed in the United States, a nominal 10% loss from its attack, which it would be reasonable to expect, would amount to \$825,000,000. annually, from the national stand point and \$31,000,000. from that of California, alone.

The single expenditure of even \$10,000,000, in attempting its eradication — and it would now appear that it should not exceed \$3,000,000. — particularly where the possibility of accomplishment seems so encouraging, would seem more than ample justification. Attainment of the objective, as has been previously stated, would seem restricted only by the degree to which all existing infestation can be found, and by the degree to which further spread can be prevented in the interim.

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## DISCUSSION

J. A. FREEMAN. What is being done to prevent reintroduction of *Trogoderma* into cleaned areas either from inside the country or from foreign countries?

H. M. ARMITAGE. No infested host material is allowed to move from any infested premise excepting under approved, officially supervised treatment. This applies also to used bags and other containers. Complete information is available on all known infested operations as a guide to operators of clean premises in securing host products.

B. SMITH. In all these huge fumigation experiments did you have any accidents?

H. M. ARMITAGE. There have been no accidents in our operations to date.



# Distribution and Persistence of Fumigant Mixtures Applied to Grain<sup>1</sup>

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## ABSTRACT

Methyl bromide, ethylene dibromide, and carbon tetrachloride (MB, EB and CT) were applied both singly and in admixture to the surfaces of grain stored in commercial warehouses and in test cylinders. Chemical analyses of the individual fumigant gases made at various levels showed that EB was strongly sorbed at surface levels and that this tendency was augmented in the presence of weed seeds of high oil content, and particularly when grain of high moisture content was present. The downward diffusion of MB was much faster and greater than that of EB under similar conditions. When CT was added, significantly higher proportions of EB and of MB penetrated to the bottom of 30-ft. grain piles, and caused increased mortality of test insects. A fumigant containing EB + CT showed greater insecticidal effectiveness than a spot fumigant containing EB + MB. This is explained partly by the improved downward distribution and persistence of EB when CT is present.

When an EB:MB mixture was applied to wheat the EB was rapidly sorbed within the first 16 hours, resulting in an appreciable reduction of the original EB:MB ratio. Analysis of the gases removed from the treated wheat in a desorption apparatus showed that the desorbed gas consisted almost entirely of EB.

From experimental evidence indicating preferential sorption of some of the components of fumigant mixtures, it is concluded that insecticidal concepts based on fixed chemical proportions do not apply in practice.

Fumigants vary not only in toxicity to insects but also in the degree to which they can penetrate to the bottom of a grain pile. Thus we might find that 12 to 16 hours after application to the surface of a 30-ft. pile of grain that fumigant A, B or C might penetrate to different depths. Such facts form the basis for formulating fumigant mixtures for application to stored grain, wherein two or more fumigants of different penetration characteristics are combined, so that the stratification trends of the individual fumigants are composited to yield a balanced or "all-purpose" mixture capable of combatting infestations at all levels.

In the course of investigation of the distribution and persistence of fumigants to control insect infestations of grain stored in elevator bins and country warehouses in Western Canada, tests were conducted with methyl bromide, ethylene dibromide and carbon tetrachloride (hereinafter designated as MB, EB and CT) applied both singly and in admixture. Tests were also made with two proprietary fumigant mixtures, namely, (a) Dawson 73 consisting of EB:MB, 7:3 by weight (applied to the surface at a rate of 6-8 lbs./M bu.) and (b) Dowfume EB-5 consisting of EB, ethylene dichloride (EDC) and CT in a w/w ratio of 7.2:29.2:63.6 (applied to the surface at a rate of 60-80 lbs./M bu.). A comparative study of Dawson 73 and Dowfume EB-5 was of particular interest, because both contained almost the same amounts of EB by weight in the dosage range aforementioned.

We determined the respective concentrations of MB, EB and CT by using chemical methods that were developed at our Laboratory. Of considerable importance, we discovered that addition of CT to EB significantly increased the amount of EB that penetrated to the bottom of a grain pile, and also produced mortality of test insects that was greater than that given by CT alone. On the other hand, preferential sorption of EB at the surface with only minimal migration towards the bottom was shown when EB was applied alone or was combined with 30 percent MB (Dawson's 73, abbreviated henceforth as D.73), or also when combined with 70 percent MB (Dawson's 37, abbreviated henceforth as D.37).

<sup>1</sup>Contribution No. 3568, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

<sup>2</sup>Chemist.

From experiments to be outlined here, we have concluded that CT in a fumigant mixture containing EB increases the toxicity of the mixture when it is applied to stored grain because it brings down more EB to the lower levels. In this respect it is much more effective than a mixture consisting of EB and MB.

Rates of penetration and persistence of some fumigants and fumigant mixtures were compared in the following manner: A series of galvanized metal cylinders, 7½ feet high x 15 inches diameter were set up. Each cylinder was filled to the 5-foot level with 5 bushels of wheat (Grade 3 Northern, 15.8% moisture, 8% dockage). The cylinders were stored in a shed at a mean temperature of 48°F. The fumigants were applied to the surfaces by removing the upper 2½ ft. section of each cylinder and adding the required amounts of fumigant that had been weighed out beforehand. The upper section was then immediately replaced, thus providing a still air space analagous to that above a pile of wheat stored in a farm granary or country annex. A departure was made for the cylinder that received MB in that the surface of the grain was covered with polyethylene sheeting of about 0.01 inch thickness. A weighed glass ampoule of MB was held outside the cylinders and the MB gas that was released upon breaking the tip and warming the walls of the ampoule was conducted through Tygon tubing placed beneath the polyethylene blanket. The open end of the tubing rested on a Petri plate.

Before applying the fumigants, screen cages containing wheat with 25 confused flour beetle adults (*T. confusum* Duv.) in each were also located at the centers of the top, middle and bottom (T, M and B) locations of the cylinders. The test cages were removed for examination at 3, 7 and 14 days after application of the fumigants.

Outlets for sampling the gases in the interstitial air were also located at the T, M and B of the cylinders, as may be seen in the photograph. The gas-air concentrations were sampled in evacuated bottles at seven different intervals, namely, at 2 hrs., 6 hrs., 12 hrs., 1 day, 3 days, 7 days and 14 days after application of the fumigants. The samples were analysed for MB, EB and CT using chemical methods that will be described elsewhere.

Table I shows the fumigants and the rates of application that were used in this particular experiment. D.73 at 6 lbs./M bu. and Dowfume EB-5 at 3 Imp. gals.

TABLE I—Rates of Application of Fumigants (5 ft. Columns of Wheat, 15.8% Moisture, 8% Dockage).

Formulations	Dosage/1000 bu.	Dosage/5 bu.
	lbs.	gms.
1. Dawson's 73	6.0	16.4
2. D. 73, plus CT (CCl <sub>4</sub> ) 1:1 v/v	10.8	29.5
3. D. 73, plus CT 1:3 v/v	20.4	55.7
4. Dawson's 37	6.0	16.4
5. D. 37, plus CT, 1:1 v/v	11.2	30.5
6. D. 37, plus CT, 1:3 v/v	21.5	58.7
7. Dowfume EB-5*, at 3 gal./M	46.2	104.8
8. Dowfume EB-5, at 1.5 gal./M	23.1	52.4
9. CT, at 2 gal./M	32.0	72.6
10. Methyl bromide**	6.0	16.4
11. Control	0	0

\*Composition (w/w) of EB-5 = 7.2% C<sub>2</sub>H<sub>4</sub>Br<sub>2</sub>, 29.2% C<sub>2</sub>H<sub>4</sub>Cl<sub>2</sub>, 63.6% CCl<sub>4</sub>. Sp. gr. of mixture = 1.54.

\*\*Surface of grain covered with polyethylene sheeting.

(46.2 lbs.)/M bu. are close to commercially recommended dosages. At these particular rates of application the gross EB potential is 25% higher for D.73 than for Dowfume EB-5. Application of CT at 2 gal./M bu. is about 2/3 of the dosage that had been recommended at one time.

In a subsequent experiment the general distribution patterns of EB applied alone and in combination with CT were mapped, and these confirmed the trends developed by D.73, D.37 and Dowfume EB-5.

The MB content, expressed as mg./l. of interstitial air, was plotted as a function of time at the T, M and B respectively of five of the test cylinders. We obtained clear indications that the addition of CT to both D.73 and D.37 increased the amount of MB at the three locations. The gas concentrations after 7 days were uniformly low and showed no significant change.

The MB concentrations of the D.73 treatment were not particularly high at any time. This appears to be related to the low content of MB in the D.73 formulation (30%), and to the probability that some MB had escaped into the outer atmosphere before or during application, thus making even less MB available for penetration. This was shown by the higher MB concentrations yielded by D.37, which contains 70 percent MB. The MB concentrations yielded by 100 percent MB at 6 lbs./M bu. were greater, penetrated deeper and lasted longer than those of D.73 or D.37. However, apart from the larger amount of MB initially present (6 lbs./M bu. vs. 1.8 and 4.2 lbs. respectively for D.73 and D.37) perhaps the higher concentrations were due in part to the plastic blanket that covered the surface of the wheat that was treated with the MB.

The concentration-time relationships of EB were likewise determined at the T, M and B of five of the test cylinders. The curves that we obtained showed the strong sorption of EB at the surface of the column, as indicated by the low levels of EB at the M and B locations after D.73 and D.37 were applied.

There was a marked jump in EB at all three levels when CT was added, 1:1 by volume, to D.73 and D.37. We obtained the same general effect when CT was added 1:3 by volume, and with various EB-CT combinations.

At all levels, the EB concentrations yielded by Dowfume EB-5 were notably high, remained so for at least 24 hours, declined somewhat by the 3-day period, after which they levelled off. The considerably greater EB-air concentrations shown at all levels by Dowfume EB-5 as compared with D.37 is, we feel, mainly due to the presence of CT in the formulation, although we also acknowledge the role of EDC in this regard. Nor do we overlook the fact that  $7\frac{2}{3}$  times more fumigant by weight (46 lbs./M bu. vs. 6 lbs./M bu.) was applied in favor of the Dowfume EB-5. However, in using these commercial recommendations, we actually deposited about 25 percent more EB when D.73 was applied, so that any apparent experimental bias is unintentional.

With reference to our findings on CT-air concentrations, the CT concentrations of the D.73-CT mixture proved to be significantly higher than that of the D.37-CT mixture. We have no reasonable explanation for this result.

The CT concentrations shown by Dowfume EB-5 were considerably higher than those of the D.73-CT and D.37-CT mixtures. Those of CT applied alone were higher still. CT alone showed only moderate and slow-acting insecticidal power. In this regard, the median lethal concentration ( $LC_{50}$ ) of CT vapor to adults of *T. confusum* was 185 mg./l. for 5 hrs., according to Shepard, Lindgren and Thomas (compare with Ferguson and Pirie's 275 mg./l. for a 24-hr. exposure of granary weevil adults). On the other hand, the  $LC_{50}$  of EB against *T. confusum* adults is 14 mg./l. for a 5-hr. exposure (Young and Cotton).

The bioassay results, taken over a 7-day period, and using *Tribolium confusum* adults, for the D.73 treatment support the chemical assays that were made on the distribution patterns of the fumigant mixtures. The effectiveness of Dowfume EB-5 was quite evident, as was the increase in effectiveness when CT was added to EB or MB-EB mixtures.

D.37 was more toxic (100 percent at both 3 and 7 days) than D.73 at similar locations. The greater content of MB in the D.37 formulation would account for this.

CT applied alone was relatively ineffective at 3 days exposure. The mortality increased somewhat at 7 days, and reached 100 percent at 14 days. This supported our general impression that CT applied alone is not a particularly effective grain fumigant.

One would have to qualify that statement, however, since by maintaining a high concentration of CT vapor for a long period, greater toxicity may be obtained.

By applying differences in reaction rate, MB may be separated from EB, EDC and CT in admixture. Thus, MB reacts quantitatively with monoethanolamine at 3°C. in 16-20 hrs., and under these conditions the reaction of EB, CT and EDC is completely suppressed. Hence MB can be selectively measured while coexisting with the others. To separate EB from CT or EDC, we hydrolysed the sample at 100°C. for 3 hrs. and then selectively oxidized the bromide to bromate, and calculated the latter as EB. We also determined the total halide and deducted therefrom the values of EB and MB, and thus obtained CT, or CT + EDC, by difference. The method has good sensitivity and reproductibility, and uses a polarographic method of ampèrometric titration with a rotating platinum electrode. I should add that we have not yet developed a satisfactory separation of EDC from CT by methods based on alkaline hydrolysis, and therefore our CT values for Dowfume are high because EDC is included therein.

As an additional laboratory technique for determining distribution patterns and sorption rates, we used a 50-gal. steel drum with removable cover. The cover was fitted with openings for gas-sampling tubes, a manometer, thermometer, wiring for a fan, a tube connected to a vacuum pump, and an opening for the introduction of fumigants. A small negative pressure was first obtained with the vacuum pump and, with the fan in operation, the fumigant was introduced from the outside with the aid of heat, if necessary. Air was readmitted to restore the internal pressure in the drum to atmospheric pressure. Samples were then taken in evacuated bottles to check the gas-air concentration.

In conducting sorption experiments, wheat or flour was placed in a large covered and ungreased desiccator the knob of which was attached to a steel wire that led upwards through a tight sleeve located in the cover of the drum. After the fumigant was introduced and circulated, the desiccator cover was raised by lifting the wire, and gas samples were taken at predetermined intervals.

By plotting the values of gas concentrations vs. time, we obtained information on the sorption characteristics of the system in question. As an example, Table II shows

TABLE II—Changes in EB/MB Ratio (MB = 1.0) in Air After Various Periods of Exposure.

Days of Continuous Exposure	H <sub>2</sub> O Content of Wheat		H <sub>2</sub> O Content of Flour	
	16.7%	12.0%	12.0%	11.25%
0.0	6.60	2.95	1.00	1.35
0.67	1.95	1.70	0.52	0.83
1.0	1.79	1.43	0.54	0.76
2.0	1.50	1.38	0.47	0.73
3.0	1.18	1.40	0.46	0.50
4.0	1.08	1.42	0.41	0.50
5.0	0.92	1.29	0.36	0.45

the changes in EB/MB ratio (with reference to MB = 1.0) when various mixtures of EB + MB were applied to wheat and to flour for a continuous period of 5 days in the fumigation drum shown previously. Other data, not shown here, clearly show that EB is absorbed relatively rapidly within the first 24 hrs., and that the proportion of EB sorbed is substantially increased when the moisture content of the wheat or flour is raised.

We have demonstrated by such experiments that EB:MB ratios may be altered substantially from the original proportions. Consequently, for fumigant mixtures such as we have tested, insecticidal concepts based on fixed chemical proportions need not apply in practice. Thus, if claims are made for synergistic effects for a given mixture of insecticides on the basis of bioassay tests conducted in empty test chambers, we must

check the composition of the mixture after it is applied under field or semi-field conditions. The underlying concept is based on constancy of composition, but, as we have shown, the composition may change considerably.

The milling and baking qualities of the wheat were unaffected by the experimental fumigations. The treatments had no effect on the naturally occurring thiamine (Vitamin B<sub>1</sub>) of the wheat, and there were no marked differences in germination capacity between treated and untreated samples, except for a slight change resulting from the MB treatment, wherein some kernels had thickened root tips and reduced root length.

With regard to residues, we obtained highly variable results which are difficult to interpret. Thus in some fumigation drum experiments we obtained residues that ranged from 6.45 ppm. of bromide. When the wheat and flour were relatively dry, more of the bromide was found in samples taken from the bottom of the desiccator, whereas when the wheat and flour were comparatively moist, more of the bromide was distributed in samples taken from the top and middle areas. On the other hand, when we determined the ppm. of residual bromide and chloride in wheat fractions milled from wheat sampled at the top and bottom of the test cylinder experiments, we obtained values that ranged all the way from 0.565 ppm., depending on the nature of the fumigants that were used and the period of aeration. The residues of wheat and flour that result from the application of halogenated fumigants are largely of a volatile nature, according to our findings, and diminish upon adequate aeration.





# Susceptibility of Cotton and Jute Flour Bags to Infestation by the Hairy Spider Beetle, *Ptinus villiger* (Reit.)

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## ABSTRACT<sup>1</sup>

*P. villiger* commonly infests flour packed in cotton and jute sacks by ovipositing through the fabric. Experiments carried out in flour storage warehouses with sacklets made from seven cotton fabrics and one of jute used by the milling trade showed that finely woven cotton and sized cotton resisted infestation. Sacklets made from coarsely woven cotton and jute were heavily infested.

<sup>1</sup>Full text will be published in *Cereal Chemistry*, 1958.



Section  
on  
**FOREST ENTOMOLOGY**



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**INDEX**

	Pages
Study of Population Dynamics in Forest Entomology . . . . .	109-162
Forest Management in Relation to Cultural Control of Insects . . . . .	163-192
Forest Insect Surveys . . . . .	193-232
Insect Problems in Forest Plantations . . . . .	233-274
Chemical Control of Forest Insects by Aircraft. . . . .	275-316
Biological Control of the Balsam Woolly Aphid (See Section on Biological Control, Vol. 4, pp. 777-826)	
General Papers . . . . .	317-440





# On the Regulation of Insect Populations

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## ABSTRACT

Despite their enormous capacity for multiplication, the population density of many noxious insects normally remains fairly stable at a low level. The regulation processes responsible for this phenomenon must be dependent on the population density of the species concerned. It is supposed that this density dependency is brought about by "density-dependent factors" and "delayed-density-dependent processes".

Regulation at a high level may take place as a result of starvation, emigration, or factors within the population as described by Pearl. Regulation at a low level may take place by predators acting as delayed-density-dependent factors ("modifiable factors" of Voûte), predators specialising on prey concentrations (usually when there is a shortage of food), and diseases.

Parasites will regulate their host at a fixed level only in combination with density-dependent factors, which quench the oscillations with ever-increasing amplitudes otherwise inherent in the host-parasite relationship.

This quenching principle may be of great importance for a proper understanding of biological control by parasites, and also of the part played by predators such as birds, ants, and perhaps small mammals in the prevention of outbreaks. The importance of the latter would then not so much lie in their direct effect on the prey population, but in their intervention in the relationship between the prey and its parasites, thus enabling the latter to regulate that prey species at an acceptable level. Further investigation into the "quenching" principle might therefore greatly improve our insight into the mechanisms of biological control.

The regulation of the population density of insects has for a long time attracted the attention of workers in applied entomology. There was a time when the term "biological control", that means regulation of the density of a noxious insect by means of its natural enemies, was almost magic. As the success of the biological control method was not general and was for the greater part limited to tropical islands, and as the chemical control of insects grew more and more successful, the belief in "biological control" decreased. In forest entomology, however, interest in biological — or perhaps one may better call it ecological — control of noxious insects remained on the same high level, even though chemical control of forest insects is very common. The interest in ecological control in the forests is due to the fact that it is easier to establish a stabilized community in a forest than in an agricultural area with annual crops and crop rotation. Orchards lie between forests and agriculture in this regard and it is remarkable that among fruit entomologists much work has been done or is in progress on ecological control (Pickett, 1949; Smith, 1935; Flanders, 1955; Clausen, 1940).

For biological control, non-indigenous enemies are almost always used, owing to the fact that, if the indigenous parasites or predators are able to control an insect, this insect should not have manifested itself as a pest. In a very few cases studies were made of the reason for the failure of the indigenous enemies of the noxious insects. In these cases the situation was not very complicated. So Hazelhoff (1928) observed that *Encarcia flavoscutellum* Zehnt, a parasite of the sugar-louse, *Oregma lanigera* Zehnt, was not able to follow its host quickly, so that in new plantations the host arrived at first alone. A severe outbreak was almost always the result. If later the parasite arrived also it was able to control its host. So the slow migration of the parasite was the cause of its failure as a regulation of the host.

I observed that *Ageniaspis*, a parasite of *Phyllocnistis citrella* Staint, could only find its host if the cuticula, by which this leaf-miner is protected, was thin, that means if the leaves were shaded. So in shaded nurseries the parasite could control the miners; if, however, shade was absent, a severe outbreak could take place (Voûte, 1935a).

Schneider's (1939) research in the gambir insects may also be mentioned. He observed that in the neighbourhood of the virgin forest the gambir plantations were never defoliated by a caterpillar, *Oreta carnea*, which was very noxious at some distance from the forest. This was due to a lack of parasites, coming from the forest.

Sometimes an outbreak is due to the application of insecticides or fungicides to control other noxious insects or diseases. Schneider (1914) mentions 54 mites or insects which increased in numbers after spraying. In some of these cases it was proved that the death of parasites or predators was the cause of the increase of the population-density of the noxious insect. See also Pickett and collaborators (1949), who reduced the spraying programs so that the natural enemies could maintain themselves in larger numbers. Good harvests were obtained in this way.

Observations like these, although not scarce, remain incidental and further research is necessary for a better understanding of the question why sometimes parasites and predators fail and in other cases they prevent outbreaks. The science dealing with the problem of the regulation of the population-density is called population dynamics.

Population dynamics is a young science and its development meets with many difficulties. As long as it is possible to work with insect populations in the laboratory, good results may be obtained. But the aims of this science must be to explain phenomena in the field. In the laboratory one may eliminate the greater part of the factors influencing the population density and control the other ones. In the field, however, it is very difficult to do so. Here we have to deal with all factors present.

The work of Varley (1947) on the knapweed-gall-fly and that of Klomp (1956) on *Bupalus* proves that an analysis of the situation in the field is quite possible.

Such an analysis, which will be of great interest for the further development of population dynamics, is made of some Canadian forest insects (e.g. the spruce budworm by Morris and associates).

As long as the data collected are insufficient to make a solid basis for the new science, working hypotheses have to be made on the available data, collected in the laboratory and in the field, on deductions from these observations, and on reasonable presumptions. This should be understood with regard to the relative value of the hypotheses, and also, the relative value of the conceptions developed hereafter.

With regard to the relations of insects and their parasites or predators, important working-hypotheses have been made by Smith (1935), by Thompson (1929), and by Nicholson (1933). According to Klomp (1956), the last two hypotheses are both justified and not contrary to each other. Such working-hypotheses are very useful for the development of our knowledge. They inspire experimental work and also the making of correlation-observations.

The danger of a hypothesis is that one may be reluctant to abandon it. But at the moment new observations give data that do not agree with the hypothesis, one has to do so, and if possible replace it by a new one, that conforms better with the new data. A hypothesis must develop with the development of the science. It is no more than a momentary conception of the problem as a whole. The hypothesis accepted by the author at this time is, notwithstanding the objections of Andrewartha and Birch (1954), that of the density-dependent factors regulating the population density of insects (Smith, 1935; Solomon, 1949).

Schwerdtfeger (1935) measured the population density of some forest insects by counting the number of pupae in the soil. The results were remarkable for they indicated that the average density of an insect is over a long period the same in the same type of forest. The level of the density is a low one. At the moment of an outbreak, however, it may exceed this level by 100 times or more. So there appears to be a constant hypothetical level for every forest insect around which the density oscillates irregularly. If this is true, there must be a tendency for mortality to increase and for reproduction to decrease, or for other processes diminishing the population density to increase, as the population density exceeds the hypothetical level. So the processes keeping the density at its special level must be dependent on the population density itself, i.e. they must be density-dependent.

Not every factor influencing the population acts density-dependently on mortality and reproduction. But, if the whole complex of factors regulates the population density, this regulation is due to these density-dependent factors of the complex. Also factors like weather acting independently of the population density may cause a heavy mortality. In many cases mortality caused by climate is so heavy that authors like Bodenheimer (1928) and Uvarov (1931) argued in their earlier publications that regulation must take place by their action. But if it is improper to say that these density-independent processes bring about regulation at a special level, it is clear that they will be able to influence the density at which the level is maintained by the density-dependent factors. There are many observations indicating that in the field the level at which density is regulated is the result of the interaction of the population and the whole complex of reduction-factors (Schwerdtfeger's "gradocön").

Schwerdtfeger (1935) observed that this level differed in different types of forest; and it is observed too, for example, that in Scotchpine forests the level of *Bupalus* varies in countries with different climates. If the level is determined by the whole complex of factors dealing with the population, this level varies from year to year, because the weather never is the same in different years, and the density-dependent processes will bring the population-density every year to another level.

### DENSITY-DEPENDENT FACTORS

Density-dependent factors are measured in their influence on the population, that means in percentage mortality, etc., not in factor-units (e.g. density of a parasite population).

From the literature many density-dependent factors are known:

1. Population-density itself, or crowding (Pearl, 1926; Cromby, 1943).
2. Food (or shortage of food).
3. Polyphagous predators, specialising on a more abundant prey. Mortality among the prey increases with increasing density until a maximum is reached after which satiation of the predator takes place and mortality decreases. So mortality can be expressed by an optimum curve. During the range of increasing mortality the predator acts as a density-dependent factor; after the maximum is reached, it is no longer density-dependent, but reverse-density-dependent, e.g. caterpillar-titmice relation (Tinbergen, 1955).

4. Cannibalism (Park, 1938).

Other types of density-dependent processes are known to reduce population density:

1. Emigration, increasing with an increase of population-density (grasshoppers, Uvarov, 1933; *Calandra*, Voûte, 1937).
2. Degeneration (Franz, 1949).
3. Limitation of hiding places (Andrewartha and Birch, 1954).

### DELAYED-DENSITY-DEPENDENT PROCESSES

Some factors are influenced by the population density, not at the moment but afterwards (Solomon, 1949):

1. Synchronised parasites (monophagous parasites, many times used for biological control); above a certain level of the host population, the parasites increase in number, until at the end they overtake the host (Nicholson, 1933; Thalenhorst, 1941; Besemer, 1942).
2. Synchronised predators (e.g. ladybirds; Clausen, 1940).
3. Diseases (Franz and Krieg, 1956; Steinhaus, 1949).

### REGULATION AT A LOW LEVEL

Only a small number of these processes are able to regulate the population at a low level:

1. From the density-dependent factors, only the predators specialising on concentrations of a prey, if and so long as they are able to cover the whole area (for example and literature, see Voûte, 1951).

2. From the delayed-density-dependent processes, the diseases and the synchronised predators (e.g. ladybirds, in many cases used for biological control of plant-lice).

3. From the other processes, emigration (e.g. *Calandra oryzae*) and a limitation of hiding places. The limitation of hiding-places as a regulation factor is insufficiently known. In most cases only an absolute protection is taken into account. There are, however, indications that also more and less favourable places on a tree may act regulatively in combination with weather-factors. Thus, it is observed that *Lygaeonematus abietinum* (Htg.) leaves certain branches of a tree during special weather conditions. The complex, hiding places — weather or other conditions, is open for intensive and promising research.

### REGULATION AT A HIGH LEVEL

Regulation at a high level is also possible:

1. From the density-dependent factors, food shortage (but only in those cases in which the shortage of food does not occur to such an extent that the whole population dies by starvation, e.g. *Euproctis chrysorrhoea* (L.) (Fransen, 1942) and *Tortrix viridana* (L.), crowding, and perhaps degeneration (Franz, 1949; *Cryptorrhynchus gravis* (F.) Voûte, 1935b).

### FACTORS THAT FAIL TO REGULATE AT A FIXED LEVEL

Other factors dependent on the population density are not able to regulate, or to regulate at a fixed level:

1. Among the density-dependent factors, food shortage generally causes a starvation of the greater part of the population of forest insects, reducing the population from a very high (outbreak) to a very low level. The greater part of the polyphagous predators (e.g. titmice; Tinbergen, 1949) are not able to regulate at all. In a certain range of the population density they can only slow down the increase somewhat.

2. From the delayed density-dependent processes, the parasites are, according to Nicholson, not able to regulate on a special level; theoretically they cause, in the host population, oscillations with an increasing amplitude. That means they cause outbreaks.

However, many successful cases of biological control of insect pests by means of introduction of parasites are known (Tothill, Taylor and Payne, 1930). This is contrary to the theory of Nicholson and very difficult to understand with the aid of the theory of Thompson. There must be a process quenching the increasing oscillations. Nicholson gives some possibilities for it; but they are not sufficient.

Tinbergen calculated that every density-dependent process, also those that are not able to regulate the population themselves (e.g. titmice), may quench the oscillations in the Nicholson system. By this discovery, the contradiction between the Nicholson theory and the observations in nature is eliminated. In a forest it means that birds, whose predation acts on the mortality of the caterpillars as an optimum-curve, may have the ability to quench the oscillations caused by the activity of special parasites. The same thing may be expected from ants acting as density-dependent factors but not being able to regulate the population; from food-shortage (in the publication of Utida, (1955), a curve is given, that may be an experimental proof of this relation); and from crowding and emigration. According to the calculations of Tinbergen (1955), parasites are potentially able to regulate the population density at a low level if acting in combination with these quenching influences. In this way the success of biological control through introduction of parasites may be understood: a quenching, not regulating, process was present, and the regulating parasite was imported.

Perhaps the promising results with the artificial increase of the bird population on some pests *Tortrix viridana* (L.) may be explained in this way.

Much research will be necessary to get a clearer idea of this type of regulation. The late Professor Tinbergen published a compilation of his results in Dutch. Prof. H. Klomp will publish the calculations in a more detailed form.



Apart from those density-dependent processes, quenching may also result from immigration, by which an extermination of the host is prevented. In plant-lice an almost continuous immigration is observed. I observed the same thing in *Phyllocnistis citrella* (Staint) in shaded nurseries (Voûte, 1935a). In this case the parasite population could persist with a parasitization of 100%. The places from which immigration took place could not be reached by the parasite. In the case of *Phyllocnistis* the immigration rate was so high that notwithstanding the 100% parasitization considerable damage was done to the young plants in the nursery.

There will be other quenching principles, not mentioned in this paper. Further research on this principle will be of great importance for biological control of our insect pests.

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## DISCUSSION

R. F. MORRIS. During outbreaks of some insects, such as the spruce budworm, high populations may be maintained for 10 years or more, providing a superabundance of food for birds and other predators. If such predators are important in damping oscillations of forest insects, why is it that other insects do not reach high population levels during these periods when predators have more food than they can possibly consume?

E. T. G. ELTON. Other quenching mechanisms may be responsible for the prevention of outbreaks of the other insects (other possible quenching mechanisms were mentioned in the paper). In the case of titmice the desire for a varied diet may cause them to take sufficient numbers of other prey species.

# Is the Density of Animal Populations Regulated by Mechanisms or by Chance?

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## ABSTRACT

By regulation is understood the maintenance of a more or less strongly fluctuating condition, but with a long-term average of population density which remains constant. On the basis of theoretical deliberations, field investigations and experimental research, the view has arisen that the possibility of such regulation is dependent on the presence of a mechanism whereby a rising density will be stopped and reversed automatically by opposing factors. But more recent research on the causes of fluctuations in various insects has shown that, in many cases, chance influences have an essential or decisive significance, both on immediate abundance and on long-term populations. By "chance" is meant an influence which is independent of the population and of changes in its density; for example, a weather factor. In model experiments in which white and black marbles represented the promoting and opposing factors, the significance of chance in the regulation of population density was shown. It follows that an abundance which remains nearly equal for a long time can be maintained through purely chance influences, and the greater the number of chance factors to which the population is subject, the truer this is. The density of animal populations will be regulated not only by mechanisms but also by chance. According to the species and the environment, sometimes the one and sometimes the other has the greater significance. In many cases, random influences can maintain abundance at an approximately even level for as long as a decade until a special event of unusual strength permits it to rise; then a mechanism must intervene, such as food depletion through complete defoliation. The mechanism is thus like a safety device which occasionally takes over when the play of chance becomes too one-sided.

Regulating means the maintaining of a more or less varying, but on the average equal population density; in other words, the regulating influences cause the maintenance of a balance, which may be called a population balance if the equalizing of fertility and mortality within a population is meant, or a biocenosis balance in case one means the relation of numbers or of the mutual influences between the population and the other components of the biocenosis. Regulating factors become effective by depressing the density when it increases and by raising it when the abundance decreases.

Based on theoretical considerations which are supported by observations in the field and by experiments, many authors generally accept the possibility that such a regulation is bound to the presence of a mechanism, in such a manner that checking influences automatically become more effective when the abundance increases and vice versa. As an example, Nicholson (1933, p. 135) writes: "For the production of balance, it is essential that a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low. In other words, the action of the controlling factor must be governed by the density of the population controlled." Only density-dependent factors — in the broadest sense — are able to cause a balance. Influences which are independent of abundance, e.g. components of the weather, can considerably increase or decrease the density, but not in a determined manner; occasionally, they may become effective as regulators and thus assist or even replace the density-dependent or density-governed factors, but in principle the maintenance of balance will be caused by the latter.

It is proved in many cases that mechanisms regulate abundance and restore disturbed balances. The gradations of the pine noctuid, *Panolis flammea* (Schiff.), are regularly followed by an increase of the tachinid, *Ernestia rudis* (Fall.), which is promoted by the enlarged host supply. The parasite reduces the host again to a normal density; that is to say, to an average abundance that is inconspicuous for many years.

Still more clearly and impressively the action of mechanisms is seen in rhythmical fluctuations which are less characteristic for insects than for certain rodents, especially for species of the Leporidae and Microtinae. Owing to a fast succession of litters and to an early beginning of maturity, these species have a high fertility which causes a rapid increase in abundance. After it has reached a certain level, a conspicuous breakdown of the population takes place, the causes of which have been disclosed to a certain degree by the work of Green, Larsson, Chitty, Frank and other authors. The population that has increased to high abundance begins to suffer from shortage of food which first causes a decrease in weight and draws on the reserves of the body; secondly, requires increased expense of energy to get food and room; and, lastly, intensifies the intra-population competition. For the individual, this means increased activity and psychic excitements which influence the endocrine system; by way of the hypophysis the adrenal gland rind is caused to produce more adrenalin which leads to reduction of the glycogene reserves, and finally to the lethal hypoglycemic shock (Frank, 1954, p. 346-347). The interaction of high fertility and of this physiological-pathological process, called "shock disease", may be considered as a classical example of the regulation of abundance by means of mechanisms.

Even if fertility and density-bound mortality interact so clearly, influences also become effective which are by no means dependent on the population and on the changes of its density. In certain regions of Germany the field vole, *Microtus arvalis* (Pallas), shows fluctuations in a cycle of three years which is based on the mechanism described. As Maercks (1954) proved, the cycle is disturbed by influences of the weather: unfavourable weather, especially in winter, retards or totally suppresses the maximum, whilst continually favourable weather hinders the breakdown of the gradation. Weather cannot be influenced by the population or its abundance; there is no causal connection from the population to the weather although a reverse connection does exist. Therefore an influence of the weather has to be considered in regard to the population as a random factor.

All observations in the field and particularly special investigations show that chance interferes to a great extent with the development of every insect population. As one example — out of many which could be enumerated — the investigations of Subklew (1939) on the population dynamics of *Bupalus piniarius* (L.) in 1937 in the Letzlinger Heide may be cited. About two-thirds of the deposited eggs were destroyed by *Trichogramma evanescens* (Westw.), which was only possible because the weather conditions were particularly favourable and because there was a stock of other host insects which from the beginning guaranteed a high abundance of the parasite. In a forest district severely infested by *Lymantria monacha* (L.), the strange case occurred that in consequence of the prodigal eating of the nunmoth caterpillars the needles, on which the geometrids had deposited their eggs, fell to the ground and the young caterpillars hatching there perished. Without exception the caterpillars suffered severe losses by violent thunder-showers; also the pupae were parasitized in a high degree by *Ichneumon nigritarius* (Grav.), the abundance of which is dependent on the existence of other suitable host insects. In all cases mentioned the occurrence of influences caused by weather and other insects was not dependent on the *Bupalus* population, at least, not in the beginning when the first attacks of polyvoltine parasites occurred. These influences as regarded from the point of view of the population were due to chance.

In the examples just mentioned chance played a large part in the dynamics of abundance, whereas the so-called mechanisms certainly maintain balance for *Microtus arvalis* and probably for *Bupalus piniarius*. But investigations recently carried out on the dynamics of abundance of some forest insects furnish examples that the population density is governed to a great extent or almost exclusively by chance, and that mechanisms have little importance. Only two investigations may be mentioned which in a particularly detailed manner are concerned with the factors governing the abundance of the species in question.

The investigation of Heering (1956) was made on an outbreak of the buprestid, *Agrilus viridis* (L.), which from 1948 to 1951 in some regions of Germany caused severe damage in beech forests. The beetle deposits its eggs on the bark. The hatched larva enters into the bark and cuts meandering galleries into the phloem and the soft

tissues of the xylem. The entering of the larva into the phloem and its establishment there depends wholly on the vitality of the tree: the healthy plant reacts by excretion of sap which often washes out the attacking larva, or by producing a wound callus in which the intensively growing tissues squeeze the larva to death. If the plant is less vigorous, particularly after long periods of drought, the defence reactions are weaker and the larva is able to succeed in entering the tree. Beside the condition of the tree, that is to say its capacity for defence, all other factors causing mortality in the various stages of development, especially predators, parasites and diseases, cut a subordinate figure. Of decisive importance for the abundance dynamics of *Agrilus viridis* is the supply of suitable host trees. In the scope of this supply, within the *Agrilus* population a more or less intense competition may arise; that means, a mechanism may become effective. But for our considerations it is decisive that the extent of the supply depends wholly on influences which can by no means be governed by the population or its abundance. Heering proved that the cause of the outbreak of *Agrilus viridis* in Southern Germany was an extraordinary succession of extreme dry and warm growing periods in the time from 1946 to 1952. The vitality of the beeches was strongly decreased and accordingly the supply of suitable brood material was increased and taken advantage of by the beetles. When — and this is very interesting as well as important for our considerations — in the autumn of 1952 rainfall set in and the beeches regained their former vitality, they not only became unsuitable for new infestation, but even trees already infested became able to drown the larvae boring in the phloem by the stronger sap flow, so that the *Agrilus* population suffered a catastrophic setback within a short time. Consequently it was the weather which, influencing the brood fitness of the host plant, indirectly determined the increase as well as the decrease in the abundance; that is to say: chance.

The other example is furnished by an intensive but not yet published investigation by Schütte on the population dynamics of *Tortrix viridana* (L.). The eggs of the tortricid, deposited on the twigs of the oak trees, hibernate. In spring when the young caterpillars hatch they enter the buds, but are enabled to do so only when the buds have reached a definite stage of development. If this stage of development does not exist, the caterpillars perish. Therefore the abundance of the population is highly dependent on the coincidence between the hatching of the young caterpillars and the development of the buds. Both of these events depend on the weather, but not in a wholly corresponding manner; therefore the two can diverge from year to year and the coincidence can be good or bad. Besides the weather, the individual quality of the tree has a decisive importance for the development of the buds: in a stand of oak trees individuals can be observed which regularly develop their buds early in the spring or late; these relative developments are fixed genetically and differ from each other in the extremes by more than two weeks. In a stand containing equal proportions of oak trees of the different developmental types, a part of the tortricid population will find in all years the suitable bud stage, so that, as far as coincidence is concerned, a more or less level abundance can be maintained. In fact, in test stands of such a kind Schütte found a scarcely varying population density, the dynamics of which were caused almost exclusively by opponents in the form of parasitic and predacious organisms. In comparison with this, in stands preponderantly composed of one type of oaks, e.g. of late developing trees, the abundance of *Tortrix viridana* in the main depends on the good or bad coincidence between the time of hatching and the stage of buds; in such stands the population density shows great fluctuations in correspondence with the conditions of coincidence which varies from year to year; biotic factors are only of little importance, perhaps because there is not sufficient time to react upon the rapidly varying abundance of their host animals. In any case it has to be stated that the population density of *Tortrix viridana* is largely and often almost exclusively dependent first on the composition of the oak stand, and second on the weather in spring, that is to say on chance.

These and further results led to doubts as to whether Nicholson's and other authors' opinions that a balance could only be maintained by mechanisms, by processes governed by the density of the population, can be correct. The supposition arose that chance, i.e. influences entirely independent of the population and its density, more



than has been accepted until now, has a great importance also as a regulating factor. To prove this supposition, a model experiment was carried out. From the beginning it was clear that such an experiment could only vaguely imitate the real circumstances, but it was expected that it could help to give an answer to the question asked.

The factors influencing the population were represented by marbles. White marbles represented favourable factors increasing population, black marbles represented unfavourable factors decreasing population. The marbles were put into a pot and taken out at random.

To carry out the experiment, the following numerical suppositions were made. The initial density of the supposed population is 10. Every white marble doubles the respective density, every black marble halves it; in other words, the arithmetical factor that the density has to be multiplied by, is 2 for the white and  $\frac{1}{2}$  for the black marble. Since in the course of a long time the population density remains equal, that is to say promoting and checking factors compensate, the number of the white and black marbles used has to be equal, 20 of each sort were put into the pot. Within a generation, 19 factors became effective; consequently 19 marbles were taken out at random and, after the arithmetical factor was determined from the portion of the white and black ones and was multiplied by the population density, they were put back into the pot, so that the original number of 40 marbles was always maintained.

The procedure may be illustrated by an example: The first 19 marbles contain 9 white and 10 black ones; 9 white and 9 black marbles compensate, one black marble remains; accordingly the initial population 10 is multiplied by  $\frac{1}{2}$ , the second generation begins with the density 5. The second time, 11 white and 8 black marbles are taken

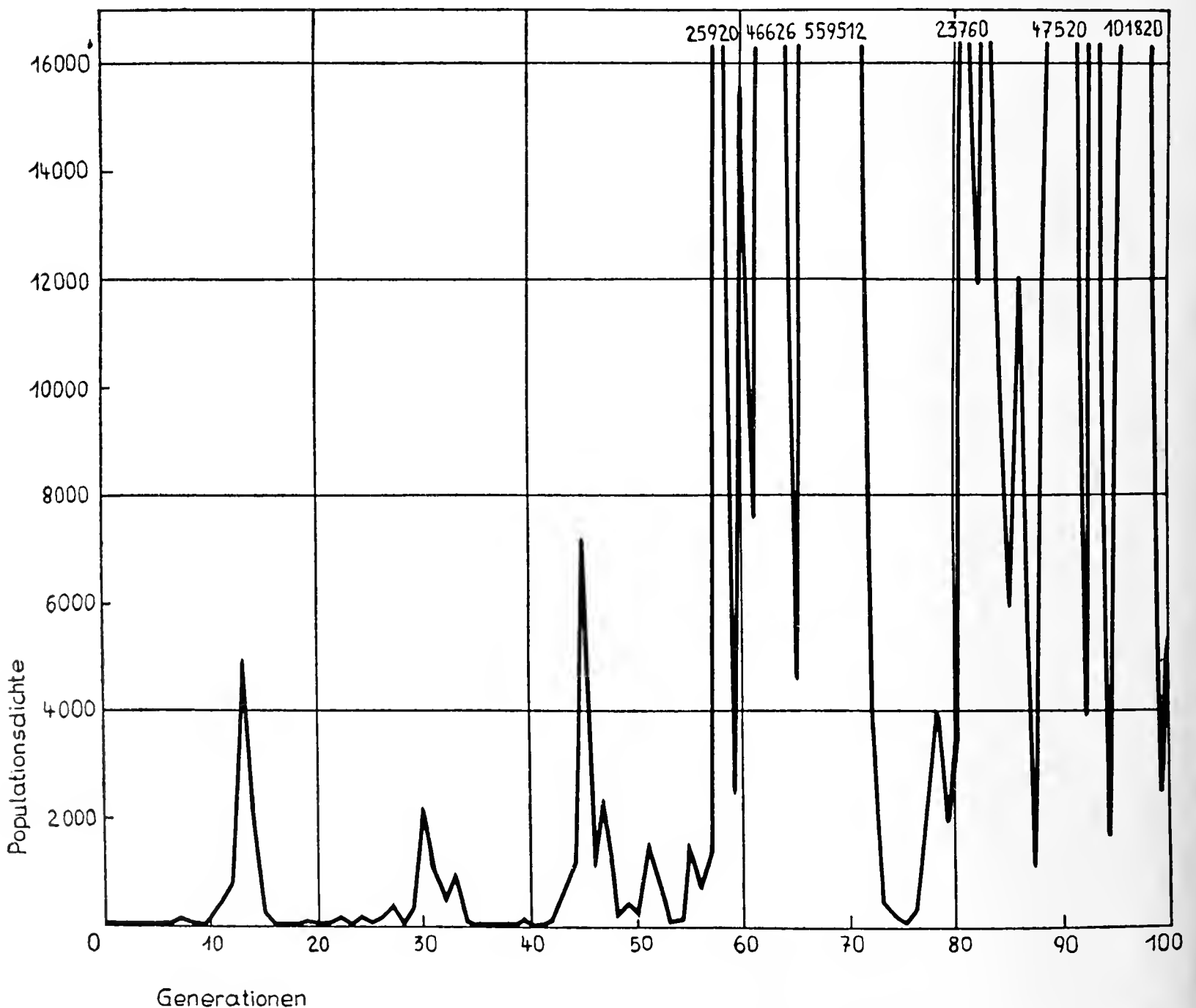


Fig. 1. Fluctuations in numbers in a model experiment during 100 "generations". Chance factors, only, are involved. For explanation, see text.



out; 3 remaining white marbles yield an arithmetical factor of 6; the population density 5 increases to 30. And so on.

This was carried out a hundred times, simulating a succession of 100 generations. The result is illustrated in Fig. 1. Promoting and checking factors acting at random result during 57 generations in densities varying to and fro, showing also greater deviations to higher abundance, but always returning close to the initial density. In the 58th generation an enormous raising of the density begins, the numbers remain henceforth in general on a high level, even when a severe sinking takes place in the 73rd-76th generation. The highest number reached is 559,512, the initial density was 10. This is an increase which, if we consider the real case of a forest insect, e.g. *Panolis flammea*, lies beyond every possibility. The food supply, ever so large, but always limited, does not allow it.

Therefore it was supposed that, if an abundance of 10,000 is reached, the present food supply will no more be sufficient and the population density will decrease to the initial number 10 in consequence of deficiency of food through defoliation. Thus a mechanism is inserted into the play of chance: self-limiting of the abundance by food competition. Fig. 2 illustrates the result of this change: up to the 57th generation the graph runs as in Fig. 1; the increase in the 58th generation is limited at 10,000 — defoliation occurs, the population density decreases strongly because of deficiency of food — and the 59th generation begins again with the density 10. In the following generations the population density remains relatively low up to the 100th generation when the test was finished.

Anyone who is well acquainted with the numerical course of arrhythmical fluctuations in the field will be impressed by the trend of the graph in Fig. 2: it resembles

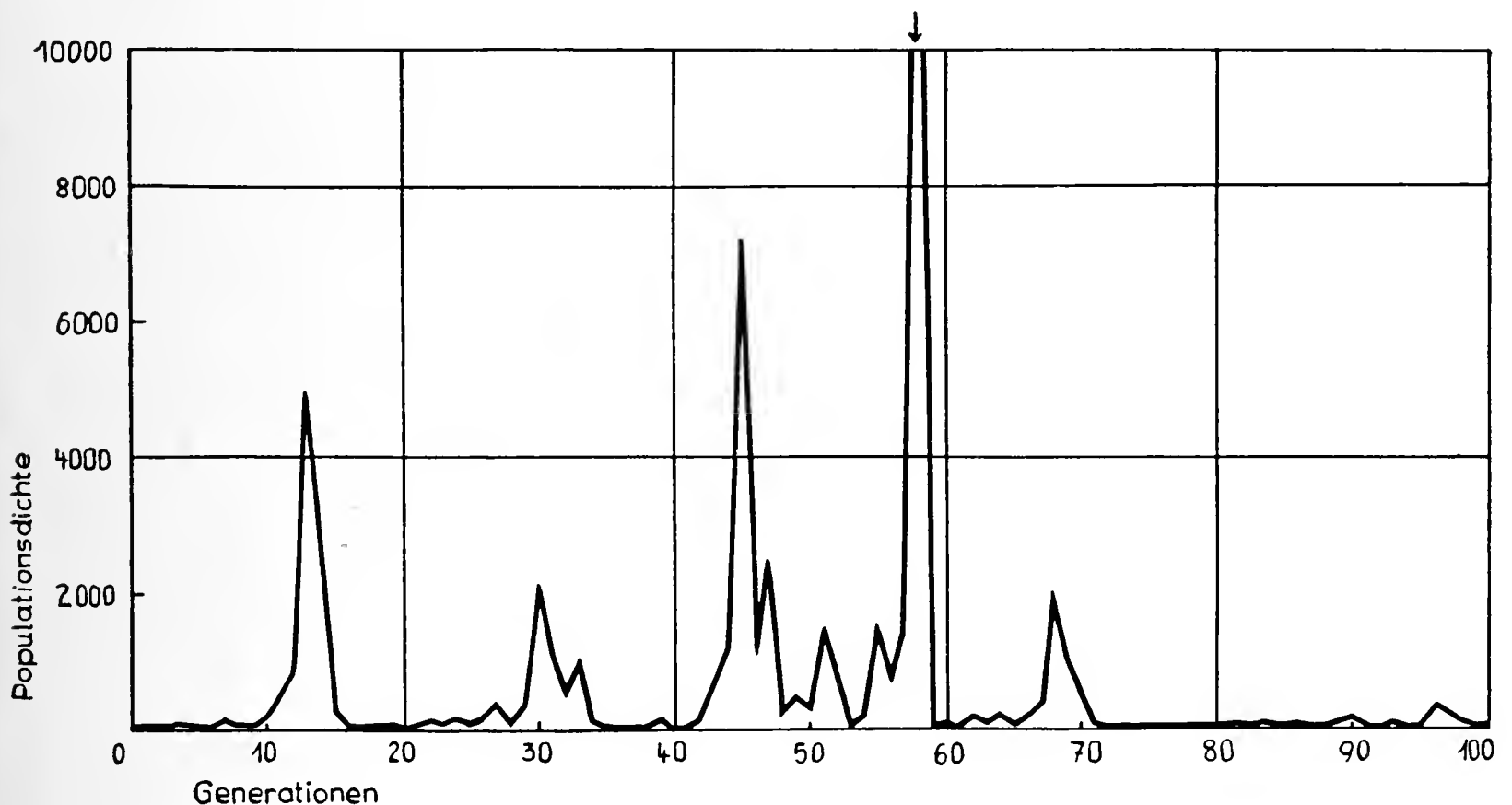


Fig. 2. Fluctuations in numbers in a model experiment during 100 "generations". In addition to the play of chance factors, a controlling mechanism is introduced at the population level of 10,000. For explanation, see text.

exactly the graphs which were drawn for forest insects on the strength of annually repeated samplings. Fig. 3 shows such graphs already published Schwerdtfeger (1941) for the 3 species, *Dendrolimus pini* (L.), *Panolis flammea* (Schiff.), and *Bupalus piniarius* (L.) which are important injurious insects in Germany. The graphs running through a period of 60 years or generations are based on samplings carried out every year in the winter in the same stands of the Letzlinger Heide, where caterpillars or pupae hibernating in the ground were found. The likeness of these graphs with those obtained by the test with the marbles cannot be overlooked and should lead to earnest thinking. If one could conclude from the resemblance of the phenomena a likeness of

the causes, one would infer that the fluctuations of *Dendrolimus pini*, *Panolis flammea* and other insects are affected almost exclusively by chance and that only occasionally, perhaps once in 100 generations, a simple mechanism represented by food deficiency is necessary to maintain the population density in balance.

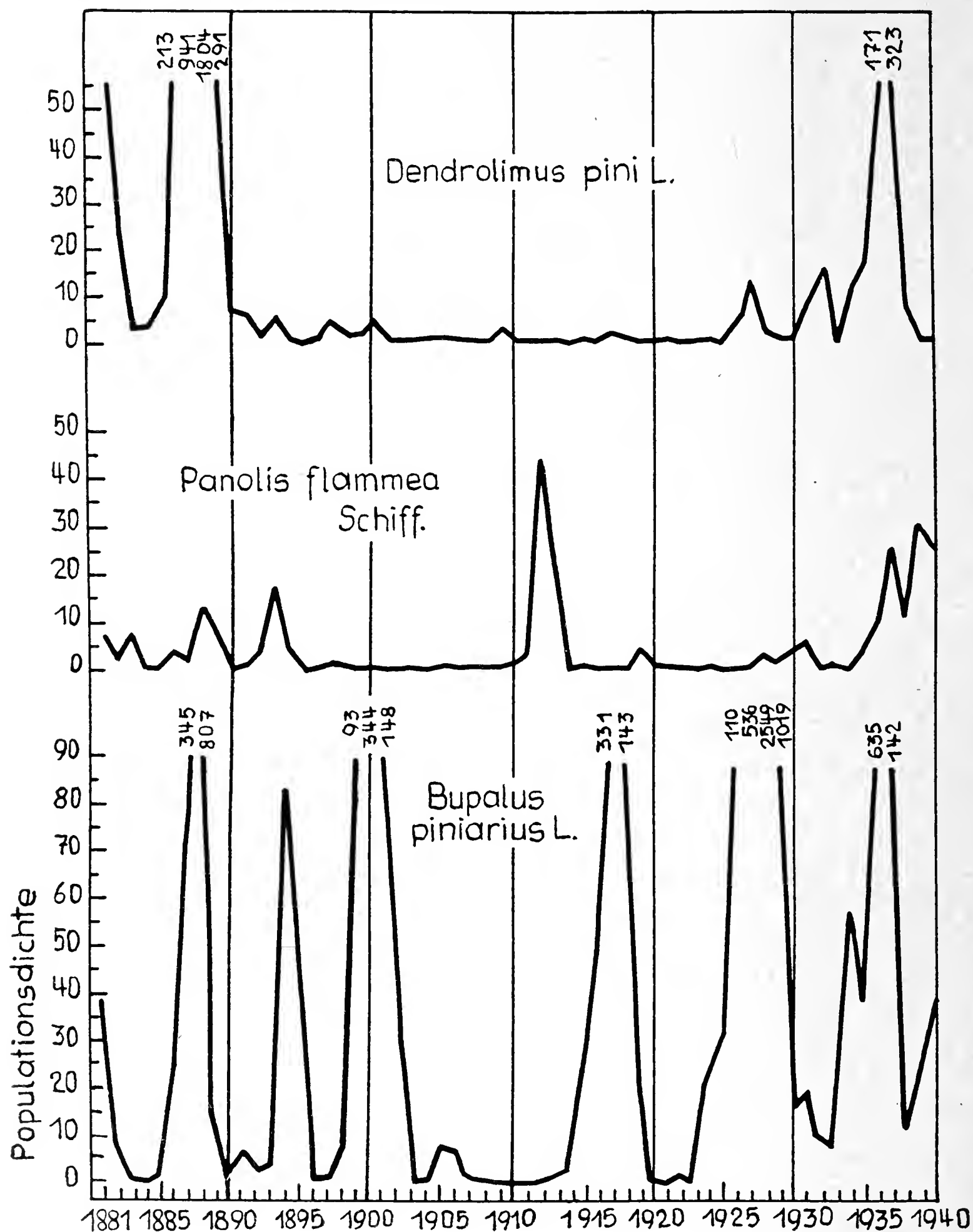


Fig. 3. Population fluctuations of three forest insects in Germany, 1881 to 1940, from Schwerdtfeger (1941).

The highly interesting result of the first model experiment caused further experiments of the same kind. To extend the questions asked, the presuppositions were varied. There is not enough space to present the results of these experiments in detail; this must be reserved for a separate publication. Only the more important results will be enumerated:

(1) The other graphs obtained resembled, too, those shown in Figs. 2 and 3, provided that at a certain high level a reduction of the population density to the

initial abundance as a result of food deficiency was supposed. Therefore, at high levels the occasional occurrence of a mechanism is necessary in order to prevent the abundance from increasing to an impossible level.

(2) In contrast, at low levels no mechanism is necessary; by pure play of chance the initial population density 10 sank in the extreme to 0.000,000,3 and then rose in the course of 21 generations to 22.6; after a further 31 generations it had increased so far that the presupposed food deficiency mechanism had to become effective.

(3) The larger the number of chance factors in operations, the rarer the necessity of a mechanism to reduce high abundance.

(4) If instead of equal numbers, more promoting than checking factors were presupposed, mechanisms must become effective more frequently than if promoting and checking factors were equal.

Summarizing, it can be concluded from the series of model experiments, that a so-called balance in animal populations can be maintained during long periods by the mere effect of chance; particularly where the number of factors influencing the population is high. A mechanism is necessary only occasionally, as if it were a fuse, to prevent an excessive increase of the population.

The critic may object that this deduction goes too far and that an abstract model experiment, a test with black and white marbles, cannot yield a positive basis for it. The objection is correct, but it is permissible to say that the authors who regard only mechanisms as regulating processes, base their opinion likewise mainly on abstraction, on experiments scarcely reproducing the real situation, and on a play with figures. Starting points of this opinion are the arithmetical formulas concerning the interaction of host and parasite populations as well as laboratory investigations with appropriate conditions. A classical example in this regard is the recent publication of Nicholson (1954), which without doubt is highly rich in ideas and very stimulating; but its extensive deductions are based after all on some laboratory experiments with *Lucilia cuprina*. The results of such experiments and of arithmetical calculations are no doubt correct for the conditions presupposed. But frequently attention is not paid to the fact that these conditions are realized in nature only rarely or never. Nature works with far more complicated conditions than are represented by the rather simple presuppositions of the experimentalists and mathematicians. Accordingly the results of the experimenters and mathematicians are clear and regular, but the phenomena in nature are confusing and often do not follow any rule. One becomes sceptical when the patterns of population change considered to be characteristic and combined in Fig. 6 of the recent publication by Nicholson (1954, p. 34) are in no case found to be realized in the fairly numerous analyses of population changes carried out in Germany on forest insects under natural conditions.

In nature, there are regularly numerous and varying factors influencing the population. They are partly dependent on the changing abundance, partly independent; they take effect on the population density partly in a promoting, partly in a checking manner. The greater the number of independent factors that influence the population, the higher is the possibility that promoting and checking factors compensate for some time, that the abundance remains in balance. Numerous observations in nature, of which only a few examples could be presented, and a series of simple model experiments permit the deduction that besides density-bound mechanisms, the so-called chance phenomena also have importance in the regulation of abundance, that the density of animal populations is governed by mechanisms as well as by chance, that the more multifarious the random play of chance becomes, the less important become the mechanisms.

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## DISCUSSION

G. C. VARLEY. I agree with most of what has been said about influence of chance. The game with marbles gives figures like those in the field — but what in the field corresponds to the use of equal numbers of black and white marbles to choose from?

F. SCHWERDTFEGER. The game with marbles should only answer the question whether pure chance can maintain a more or less equal level of abundance. It cannot substitute for investigations in the field and give information on the causes of abundance dynamics.

S. A. GRAHAM. The inference was made in your paper that weather factors operated in a random or chance manner. Does any factor operate in such a way?

F. SCHWERDTFEGER. When, after an hour, I shall leave this room and go to my residence, and a rainfall sets in, this rain is no chance in a meteorological sense, but for me it will be a chance, and a bad one. I shall get wet.

C. H. BUCKNER. There are a host of insects occurring in the forest that to my knowledge have never been known to erupt into epidemic proportions. How can these be explained in terms of the marble model described?

F. SCHWERDTFEGER. The greater the number of chance factors, promoting and checking, the more equal may be the abundance. It is possible that insects never growing to outbreaks are regulated by a very high number of chance factors; but it is possible too (and more probable) that the regulation is caused by mechanisms.

# Le Problème de la Tordeuse grise du Mélèze *Eucosma griseana* (Hübner) (Lepidoptera: Tortricidae) dans les Forêts alpines

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## ABSTRACT

The larch bud moth (*E. griseana*), a species which is widespread in Europe and Asia, causes heavy damage to various coniferous trees in the alpine zone of Switzerland, Italy, France and Austria, where it can build up very large populations. These outbreaks are periodical, the cycle lasts about 8-10 years in the Swiss cantons of Grisons, Ticino and Valais. Larches are the most severely damaged trees. The larvae devour the needles and the trees become brownish. Usually, they are not killed, but wood-growth is cut back by 30%, seed production is reduced and the forests become very ugly; this fact is important in a country which is dependent, in part, on the tourist trade.

A study was started in 1949 in the Engadine in order to get a better insight into the population dynamics of this pest. So far, only one cycle has been studied, from 1949 to 1956. The following observations have been made:

1) After the rapid decrease which follows an outbreak, the population increases continuously again to the next maximum without any period of latency. The density of the larch bud is highest in the altitude zone from 1600-2100 m. (5500-6400 ft.).

2) The outbreak is controlled by three main factors:

a. a virus disease of the granulosis type

b. lack of food

c. parasites, of which eight species play an important part (7 ichneumonids and 1 tachinid).

The virus disease destroys a great proportion of the population at the peak of the gradation; by this process, then, the parasites gain relatively great control power and accelerate the breakdown of the pest.

3) Two races of *E. griseana* can be distinguished, one on larch and the other on cembran pine. The larvae on larch are black with a black head capsule, those on cembran pine are of a pale grey colour and their head capsules are yellow-brown. This coloration does not depend on food. The adults are very similar, but these two races are ecologically and sexually isolated to a large extent.

Work along these lines is still in progress, and it is hoped that the results obtained so far will be useful in biological control of this insect.

Alors que la Suisse se trouve dans la zone d'indifférence de quelques-uns des plus grands ravageurs primaires d'Europe, tels la Nonne (*Lymantria monacha* L.), la Fidonie (*Bupalus piniarius* L.), la Noctuelle du Pin (*Panolis flammea* Schiff), elle englobe la partie la plus représentative de la zone des pullulations périodiques de la Tordeuse grise du mélèze [*Eucosma griseana* (Hb.) = *Semasia diniana* (Gn.) = *Zeiraphera griseana* (Hb.)].

Aucun autre insecte forestier primaire ne se manifeste dans notre pays par des dégâts aussi spectaculaires et avec une périodicité aussi remarquable.

*E. griseana* est une espèce boréo-alpine. Son aire de répartition s'étend des plaines de l'Europe centrale et septentrionale jusqu'à la limite de la forêt au Nord et dans les Alpes. Elle est répandue dans tout le nord de l'URSS jusqu'au Japon (Hokkaido) et elle a été introduite dans les forêts de l'Ouest de l'Amérique du Nord. Sa chenille, oligophage, est strictement inféodée aux conifères, mais l'aire de l'Insecte ne correspond à celle d'aucune espèce de cette famille botanique: la plante-hôte varie suivant les régions.



Dans les Alpes, elle attaque le Mélèze (*Larix decidua* Miller), l'Arolle (*Pinus cembra* L.), le Pin sylvestre (*Pinus sylvestris* L.) et le Pin de montagne (*Pinus mugo* Turra). Dans les "Mittelgebirge" de Saxe et de Bohême, elle est essentiellement nuisible à l'Épicéa (*Picea abies* L.) tandis qu'au nord de l'Europe on la retrouve tantôt sur le Pin sylvestre (Scandinavie) tantôt sur le Mélèze.

Dans cette vaste aire, la zone des pullulations avec dégâts est très localisée. Elle est presque exclusivement limitée à la zone alpine et s'étend de la Carinthie à l'Est jusque dans les Hautes-Alpes françaises à l'Ouest en couvrant le Tyrol, plusieurs hautes vallées des cantons suisses des Grisons, du Tessin et du Valais, une partie du Piémont et de la Lombardie en Italie, toutes régions caractérisées par un climat plutôt continental, sec et chaud en été. Dans ces régions, les forêts de mélèzes situées à une altitude supérieure à 1200 à 1300 m. sont périodiquement ravagées par la chenille de la Tordeuse dont les dégâts spectaculaires, bien connus des touristes, se traduisent par un brunissement plus ou moins marqué des peuplements. La périodicité de ces pullulations est surtout apparente dans les Alpes suisses où elle s'y manifeste par des cycles de 8-10 ans avec dégâts visibles trois années consécutives. Au Tyrol autrichien, voisin du canton des Grisons, la périodicité est moins nette qu'en Suisse et la durée des cycles plus variable.

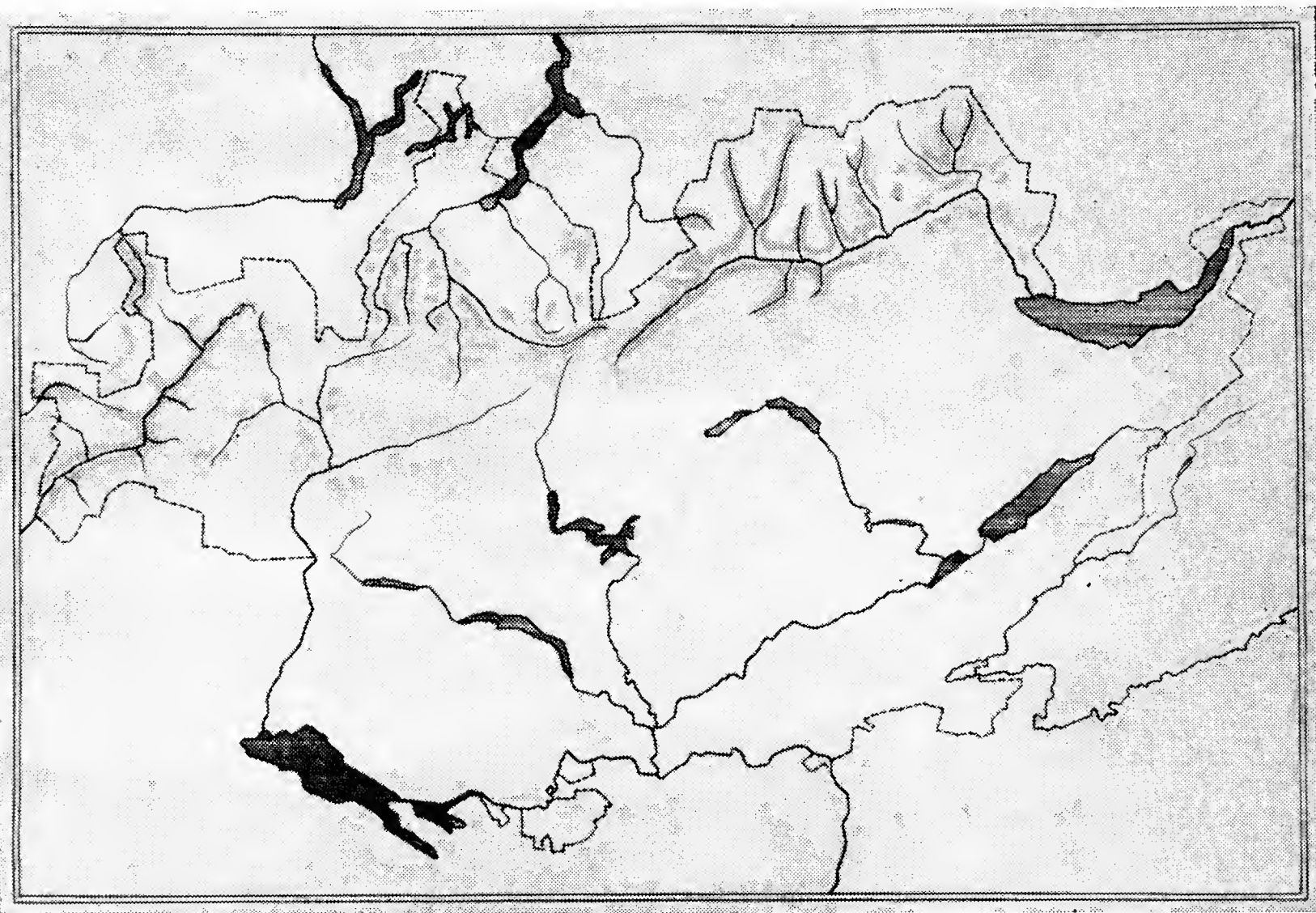


Fig. 1. Zone des dégâts de *E. griseana* en Suisse durant la précédente gradation (1953-1955).

Hors des Alpes, une pullulation grave a été observée une seule fois dans des peuplements purs d'Épicéas des "Erzgebirge" de Saxe et de Bohême, de 1924 à 1929. On a signalé récemment en URSS des dégâts sur mélèzes à une altitude supérieure à 1300 m. sans préciser si l'insecte y est un ravageur chronique ou occasionnel. Enfin, selon Keen (1952), *E. griseana* a causé récemment de graves dégâts dans l'Etat de Washington sur *Abies concolor* (Gord. & Glend.) et sur *Larix*.

Bien que dans les Alpes, les pullulations de la Tordeuse grise n'entraînent généralement pas la mort des mélèzes qui reverdissent à la sève d'août, elles n'en sont pas moins fort nuisibles. Chaque année où l'insecte cause la destruction plus ou moins complète des aiguilles, la croissance du bois des mélèzes atteints diminue de 30%. En outre, la production des graines est limitée, ce qui nuit au rajeunissement naturel du mélèze. Enfin, les forêts sont enlaidies dans des régions touristiques importantes.

Sous ce triple aspect, *E. griseana* peut être considérée comme l'un des plus importants ravageurs primaires de notre pays et la Suisse, qui se trouve au centre de la zone des pullulations périodiques, est certainement la région qui se prête le mieux à l'étude de cet insecte.

Les travaux parus jusqu'en 1948, tant en Suisse qu'à l'étranger, et dont Escherich (1931) a résumé les conclusions, n'avaient pu aborder le problème crucial de la dynamique des populations. C'est la tâche que nous avons entreprise à la demande des services forestiers, dans l'espoir qu'une meilleure compréhension du problème permettrait de prévenir ou de limiter les dégâts par des moyens biologiques ou sylvicoles. Un groupe de travail a été constitué auquel collaborent l'Institut d'entomologie de l'Ecole polytechnique fédérale, l'Institut fédéral de recherches forestières, l'Inspectorat forestier du canton des Grisons et la Station ornithologique de Sempach. Nous avons choisi comme centre de nos recherches la Haute-Engadine et un laboratoire de campagne y est installé chaque été.

Situées à une altitude de 1400-2200 m., les forêts de cette région correspondent au *Rhodoreto-vaccinietum* de la classification sociologique de Braun-Blanquet. L'arolle et le mélèze en sont les constituants essentiels, le mélèze apparaissant en peuplements purs sous diverses conditions. Dans quelques stations, le Pin de montagne, *P. mugo* forme des peuplements purs, ou mixtes avec les deux essences précitées. Vers 1600-1700 m., cette forêt mixte est en contact avec la forêt subalpine d'épicéas (*Piceetum subalpinum*) d'où la présence de peuplements de mélèzes ou d'arolles mêlés d'épicéas là où les deux associations s'interpénètrent.

Le climat de la vallée, qui correspond à l'optimum vital de l'insecte, est nettement continental, avec des hivers très froids et des étés relativement chauds. L'air y est sec, l'insolation intense, et l'on y enregistre de grosses variations de température.

La biologie de la Tordeuse grise du mélèze était connue dans ses grandes lignes, mais il s'est avéré nécessaire d'approfondir cette étude, de préciser le comportement des divers stades, tâche confiée à notre collaborateur, M. le Dr. J. K. Maksymov.

Le papillon, de coloration grise, est de moeurs crépusculaires. Il vole de fin juillet, début août à fin septembre, début octobre. Après accouplement, les femelles pondent leurs oeufs isolés ou par groupes sous les lichens (*Parmelia aspidota* Ach.) qui recouvrent les branches des mélèzes et des arolles, principalement sur celle d'un diamètre inférieur à 1 cm (Nageli 1929). Ces oeufs hivernent et dès mi- à fin mai éclosent les chenilles qui pénètrent dans les pousses mesurant 5-7 mm. Elles y rongent quelques aiguilles en s'y construisant un fuseau soyeux puis passent dans une 2<sup>e</sup> puis une 3<sup>e</sup> pousse. A partir du quatrième stade, elles rongent l'extrémité du fuseau qui se transforme en un entonnoir. Dès le dernier stade, elles se maintiennent sur les rameaux dans des toiles plus ou moins lâches d'où elles vont ronger tous les bourgeons du voisinage. Parvenues à leur complet développement, après 1 mois 1/2, elles se laissent tomber à terre pour la nymphose, qui a lieu à la surface du sol sous divers débris. Au bout d'un mois apparaissent les papillons et le cycle, résumé par le graphique en Fig. 2, recommence.

Par ce cycle évolutif, *E. griseana* constitue un matériel très peu favorable pour l'étude de la dynamique des populations. L'échantillonnage des oeufs est rendu difficile par leur localisation, celui des chrysalides par le relief tourmenté des sols alpins.

Lorsque la densité de population dépasse certaines limites, les peuplements prennent une teinte brune en juin-juillet, puis reverdissent en août, mais l'histoire des gradations s'inscrit dans le tronc par une diminution d'épaisseur des cernes des années de dégâts.

Jusqu'en 1948, on ne possédait sur l'évolution dynamique des populations de *E. griseana* que les dates des périodes de dégâts depuis 1865. Afin de connaître cette évolution, M. le Dr. C. Auer mit au point, avec la collaboration de M. le Prof. Dr. A. Linder, une technique d'échantillonnage qui consiste à mesurer les populations de chenilles par des prélèvements sur des groupes de trois arbres répartis au hasard dans l'ensemble de la zone explorée (Kalin et Auer, 1954).

Cette enquête débuta en 1949 au point le plus bas de l'évolution d'un cycle et fut renouvelée chaque année jusqu'en 1956. Elle englobe l'ensemble des forêts de la

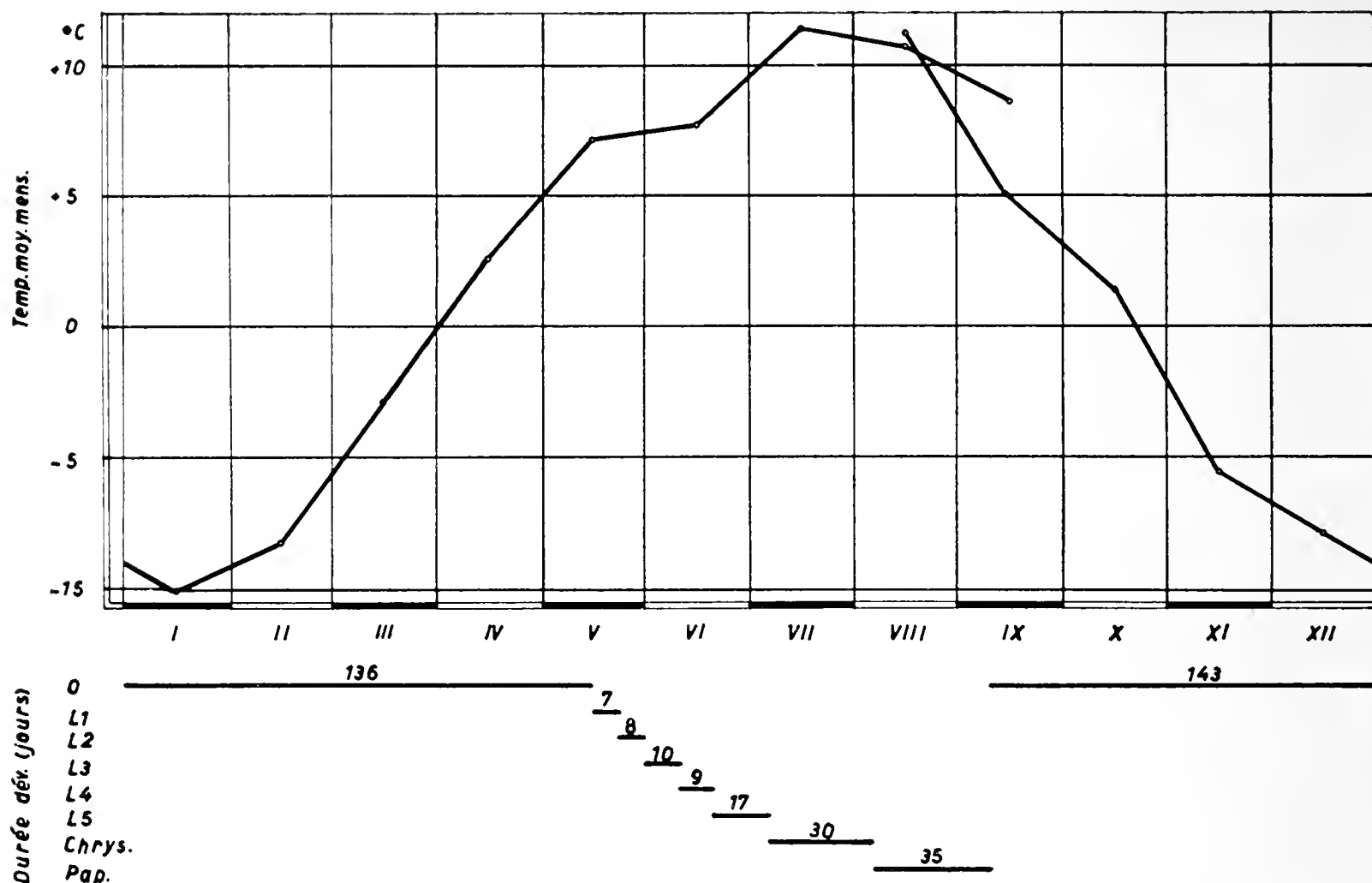


Fig. 2. Développement de *E. griseana* en Haute-Engadine (D'après J. K. Maksymov, rapport interne).

Haute-Engadine qui comptent quelque 10,000 hectares, deux bandes transversales de la vallée en Basse-Engadine, ainsi que quelques postes extérieurs à cette vallée.

Dès 1953, une intéressante collaboration avec les services forestiers et d'entomologie forestière de l'Autriche a permis de prolonger cette enquête dans cinq stations échelonnées du Tyrol jusqu'en Carinthie. Cette collaboration permettra de préciser l'évolution dynamique de la Tordeuse qui s'y poursuit avec décalage de un à deux ans par rapport à la Haute-Engadine.

La récolte du matériel est confiée à des équipes de deux hommes. L'un grimpe sur l'arbre pour y prélever 3 branches et 10 rameaux sur les 3 étages inférieur, moyen et supérieur tandis que le second examine le matériel et prélève toutes les pousses infestées qui sont envoyées régulièrement au laboratoire de campagne pour l'inventaire et l'identification de toutes les espèces de lépidoptères.

Conduite dès 1949, cette enquête a permis de recueillir une abondante documentation sur les mouvements de populations durant ces 8 années qui, du point le plus bas de l'évolution numérique, nous ont conduit à un maximum en 1954 pour assister en 1955 au début de la régression. De l'enquête de 1949, il ressort qu'au point le plus bas de l'évolution dynamique des populations, la répartition de l'insecte peut être considérée comme semi-continue. On le rencontre partout, mais en relation avec la composition et la nature des peuplements forestiers, l'altitude, l'exposition, la densité de ces faibles populations présente des variations d'assez grande amplitude, de l'ordre de 1 : 10.

Dès lors, et jusqu'en 1954, on a assisté dans toutes les régions explorées à une augmentation continue des populations à un rythme propre à chaque biotope. La Fig. 3 exprime le résultat de l'enquête pour l'ensemble de la Haute-Engadine et trois communes de la région. Ces courbes mettent en évidence, dans des régions rapprochées, des différences appréciables en relation avec des facteurs locaux et la composition des peuplements. En 1955, la régression s'amorce qui se poursuivra en 1956 sans atteindre le point de départ. Dans le cycle en question, la progression a été de 5 ans, la régression comptera au moins trois ans.

En Basse-Engadine, l'évolution dynamique est synchrone, mais la régulation s'opère à un niveau moyen un peu plus bas, tandis qu'en Autriche on en est encore

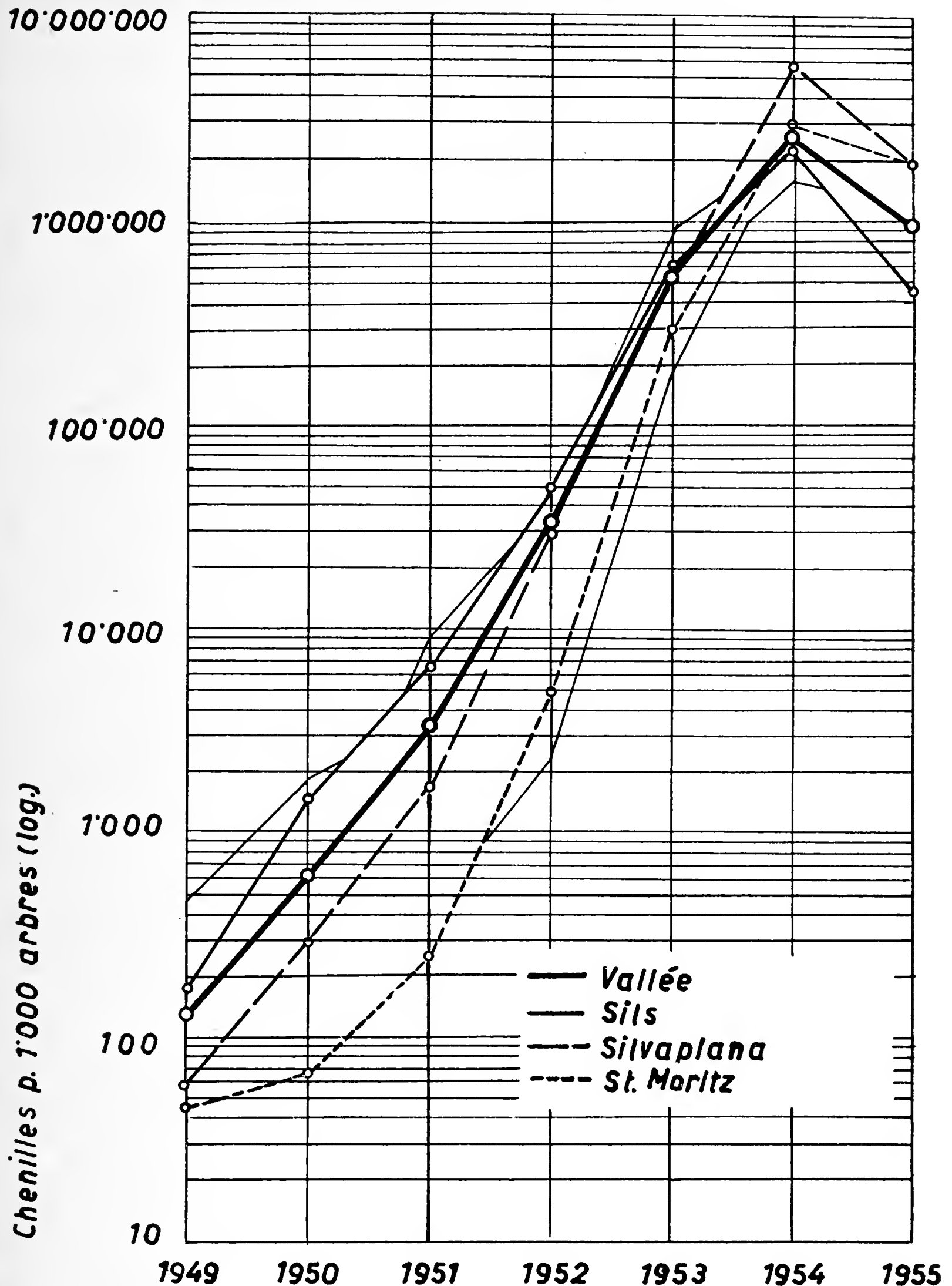


Fig. 3. Evolution des populations de *E. griseana* en Haute-Engadine (Suisse) de 1949-1955. Population moyenne de la vallée et de 3 communes. Les chiffres exprimés en coordonnées logarithmiques correspondent aux nombres de chenilles de la masse échantillonnée de 1000 arbres. La surface grise correspond à la zone de variation des populations des 11 communes de Haute-Engadine. (D'après C. Auer, rapport interne 1955).

en 1955 à la phase ascendante sans traces de dégâts, avec un décalage de deux ans par rapport à la Haute-Engadine.

L'analyse des populations montre que les densités les plus fortes en Haute-Engadine se rencontrent à l'altitude de 1600-2100 m., avec un optimum de 1750-1950 m. La nature et l'intensité des dégâts sont naturellement fonction de cette densité, mais des



populations de même grandeur peuvent se montrer plus ou moins nuisibles, ce qui indique que la voracité des chenilles n'est pas partout la même.

D'une façon générale, le brunissement se manifeste par taches, souvent à l'échelle de l'arbre, et une destruction de 75-100% des aiguilles ne s'observe jamais deux années de suite dans le même peuplement. On ne peut dire si c'est une conséquence de l'évolution autochtone ou celle d'une migration des papillons vers des zones moins dépouillées. Cette dernière hypothèse, suggérée par Standfuss (1917), apparaît vraisemblable à la suite d'une expérience de M. Maksymov. Il a montré qu'en cages d'élevages les ♀ ♀ pondent plus volontiers sur des rameaux avec aiguilles vertes que sur des rameaux dépouillés.

Au début de la phase ascendante de la gradation, on a mis en évidence une corrélation entre la densité des populations et la composition des peuplements forestiers. L'insecte est d'autant plus abondant sur mélèze que la proportion des arbres de cette espèce est plus élevée; mais au fur et à mesure que l'on se rapproche de la culmination, cette corrélation s'estompe, l'infestation sévissant aussi intensément dans les peuplements mixtes que dans les peuplements purs.

Si l'on considère que l'on a assisté dès 1949, immédiatement après la fin de la crise de la précédente gradation, à une constante augmentation numérique des populations jusqu'en 1954, on voit qu'en Haute-Engadine, comme d'ailleurs dans d'autres régions des Alpes, sinon dans l'ensemble de la région, l'évolution dynamique de *E. griseana* est caractérisée par l'absence d'une période de latence: une gradation s'amorce sitôt terminée la crise de la précédente.

L'évolution des dégâts varie dans de grandes limites d'une région à l'autre. Tantôt ils n'y sont visibles que deux années de suite, parfois même une seule année avec une intensité variable. Au-dessous d'une certaine altitude, les forêts restent vertes, mais l'enquête statistique y a mis en évidence une variation cyclique de moindre amplitude, la régulation intervenant à un niveau assez bas, phénomène que l'on peut observer en maints endroits de la zone des dégâts. C'est précisément l'intérêt de cette espèce de permettre l'étude de son évolution dynamique dans des régions voisines où la régulation s'opère à des niveaux très différents. En Haute-Engadine, la diminution de l'accroissement des populations marqua de 1953/54 le premier indice visible d'activité des facteurs de régulation dont l'action s'accentuera en 1954 et déclenchera en 1955 l'infléchissement de la courbe et le début de la régression (Fig. 3).

Quelles sont les causes principales de cette régulation? Trois groupes de facteurs importants paraissent y concourir: une maladie à virus, l'inanition et les parasites entomophages.

Dès la fin du siècle dernier, Coaz (1894) avait déjà remarqué, dans les forêts d'Engadine, la présence de chenilles atteintes d'une maladie qu'il rapprochait de la "Wipfelkrankheit" et que Del Guercio et Jahn (1949) ont considérée comme une polyédrose.

Dans le cadre de nos recherches, M. M. E. Martignoni a repris l'étude de cette maladie. Il a pu montrer en 1954 que l'on avait affaire non à une polyédrose mais à une granulose.

Après avoir mis au point une ingénieuse méthode d'inoculation orale à l'aide d'une microsonde de son invention, M. Martignoni a constaté que ce virus était l'un des plus virulents parmi ceux des insectes dont la LD 50 ait été établie. Le virus a pu être isolé et purifié. Comme celle de plusieurs polyédroses, l'étiologie de cette maladie est très étroitement liée à l'évolution dynamique de l'espèce. La granulose se manifeste de façon épizootique à partir d'une certaine densité relative des populations de la Tordeuse.

On peut se rendre compte de l'étroite relation entre l'évolution de la granulose et celle de la gradation de la Tordeuse grise en suivant le développement de la récente pullulation de cet insecte en Engadine. Les premières attaques du virus sont signalées en 1953 dans 2 stations de Haute-Engadine, où elles détruisent des chenilles du dernier stade. En 1954 et 1955, l'épizootie se généralise provoquant partout, déjà à partir du premier stade larvaire, une mortalité massive pouvant atteindre 80-90%. Il n'a pas été possible de déterminer quantitativement, en Haute-Engadine, la proportion des



chenilles détruites par le virus, mais de l'observation, il apparaît d'emblée que la granulose est l'un des facteurs les plus importants, sinon le plus important, parmi ceux qui sont responsables de la crise.

En 1954 et 1955, M. Martignoni a cherché à vérifier, en traitant des groupes de chenilles de diverses provenances, si leur susceptibilité variait en fonction de la densité des populations de tordeuses. D'après ses résultats, elle paraît varier en fonction de la progression, ce qui est très important pour la lutte biologique (Martignoni, 1957). Le caractère hautement infectieux et le potentiel épizootique de ce virus donnent d'emblée quelque espoir d'utilisation pratique.

Localement, l'inanition par manque de nourriture peut jouer un grand rôle comme facteur de régulation. Lorsque les rameaux sont complètement dépouillés de leurs aiguilles avant la fin du développement des chenilles, on voit ces dernières cheminer en grand nombre sur le tronc, en y tissant de véritables toiles soyeuses dans lesquelles beaucoup périssent. Dans certains cas, la mort de ces chenilles est associée à la présence du virus, dans d'autres cas pas. Ce phénomène du recouvrement intense des troncs par des toiles est assez exceptionnel. On l'a observé en quelques points de l'Engadine durant la précédente gradation.

Après le virus, les parasites entomophages représentent un groupe de facteurs important. Leur étude, confiée à M. W. Baltensweiler, s'est développée progressivement, car les parasites n'acquièrent qu'assez tard une certaine importance comme facteur de mortalité.

Quatorze hyménoptères et trois diptères ont été observés jusqu'à maintenant en Engadine comme parasites primaires et quinze hyménoptères comme hyperparasites. Des dix-sept parasites primaires, huit sont assez étroitement dépendants de la densité des populations de la Tordeuse et paraissent jouer un rôle prédominant au moment de la culmination. Ce sont les Ichneumonides: *Horogenes exareolata* Ratz, *Phytodietus* sp., *Phaeogenes nanus* Wsm., *Triclistus pallidipes* Holmg., *Triclistus podagricus* Grav., *Pimpla turionellae* L., et *Chorinaeus funebris* Grav., ainsi que la Tachinaire *Lypha dubia* Fall.

Dans l'ignorance où l'on était de la biologie et des rapports avec l'hôte de la plupart de ces parasites, dans les conditions de l'Engadine, il s'est avéré nécessaire de combler ces lacunes. Ce travail préliminaire indispensable n'a pas permis d'entreprendre sur une base assez large l'étude de la valeur quantitative du parasitisme comme facteur de réduction des populations. Néanmoins, des prélèvements ont pu être faits en Haute-Engadine durant les trois années précédentes, dans trois types des peuplements. L'analyse de ce matériel n'étant pas terminée, nous ne pouvons communiquer des chiffres précis, toutefois un premier examen donne des résultats intéressants. Ils permettent de constater que certaines espèces sont réparties de façon très inégale dans les divers types de peuplements. *T. pallidipes* en particulier, abondant dans des peuplements purs de mélèzes, est très rare ou absent dans certains peuplements mixtes à *Rhodoreto-vaccinietum*. Chaque type de peuplement est plus ou moins caractérisé par une constellation de parasites qui lui est propre.

Du point de vue quantitatif, les résultats acquis montrent que les parasites jouent, dans la zone de l'optimum vital, un rôle moins décisif que la granulose, au début de la crise. Ce n'est qu'en 1954 et 1955 surtout que l'on a enregistré de forts % de parasitisme, dans des populations déjà fortement réduites par le virus dès les premiers stades larvaires.

Maintenant que la biologie et l'écologie des principaux parasites sont connus, ce sera le but des recherches qui seront poursuivies durant le prochain cycle de préciser leur rôle dans le mécanisme de la régulation, sous diverses conditions de composition des peuplements, d'exposition et d'altitude.

Les prédateurs ont jusqu'à maintenant peu retenu notre attention, à l'exception des fourmis. *Formica rufa* L. est très abondante dans les forêts de Haute-Engadine. Lors de l'enquête statistique, on a pris soin de noter leur présence ou leur absence sur les arbres échantillonnés. Trois années de suite, on a pu faire cette constatation, en apparence paradoxale, que les arbres les plus visités par les fourmis étaient souvent aussi parmi les plus attaqués par les chenilles. Dans une région où presque tous les

arbres étaient visités par les fourmis, on a observé très tôt de fortes populations de chenilles. Cela tient au fait, déjà observé par Thomann (1929), que les fourmis, recherchant surtout des aphides, ne prêtent aucune attention aux chenilles tant qu'elles sont enfermées dans les fuseaux d'aiguilles ou protégées par leurs toiles. Seules les larves du dernier stade deviennent leur proie lorsqu'elles se laissent tomber à terre pour la nymphose. Ainsi, les fortes densités de *F. rufa* que l'on observe en Engadine ne préviennent pas le brunissement des mélèzes et l'on peut souvent observer des sujets entièrement bruns aux pieds desquels se trouve une grosse fourmilière.

Le rôle des oiseaux fait l'objet, de la part de la Station ornithologique suisse, de recherches qui n'en sont qu'à leur début.

Des facteurs endogènes interviennent aussi dans le mécanisme de la régulation. C'est ainsi que l'on a observé une nette diminution de la fécondité de femelles issues de chenilles provenant de peuplements entièrement dépouillés de leurs feuilles. D'autre part, des élevages de chenilles issues de populations de densités différentes ont fait ressortir, deux années de suite, des mortalités plus ou moins fortes qui paraissent relever de la constitution des populations, le phénomène étant apparu aussi bien dans les élevages en plein air que dans le laboratoire, sous des conditions constantes.

Jusqu'à maintenant, dans la nécessité où nous nous sommes trouvés de procéder par étapes, nos recherches ont été plus qualitatives que quantitatives. Ce sera le rôle des recherches futures de préciser l'importance relative des divers facteurs de résistance du milieu en nous inspirant, dans la mesure de nos modestes possibilités, des magnifiques travaux sur *C. fumiferana* poursuivis en Canada depuis plusieurs années.

Dans les forêts mixtes d'arolle et de mélèze, *E. griseana* évolue sur les deux essences, mais il est frappant de constater que les chenilles du dernier stade, issues des oeufs pondus sur l'une et l'autre, sont de coloration très différente. Sur le mélèze, elles sont noires avec tête noire, tandis que sur l'arolle elles sont grises avec deux bandes longitudinales claires et une tête jaune. La coloration des chenilles ne dépend pas de la nutrition; elle est fixée héréditairement. Les papillons sont morphologiquement très semblables, mais l'étude biologique des deux formes a mis en évidence un isolement écologique et probablement sexuel assez poussé. Les courbes d'éclosion des jeunes chenilles sont nettement décalées l'une par rapport à l'autre, en relation avec le débourement plus tardif de l'arolle. Des essais de ponte en cage d'élevage ont fait ressortir une très nette sélection de l'hôte, ce qui explique la répartition des chenilles dans la nature. En laboratoire, avec choix des deux hôtes, plus de 90% des oeufs ont été pondus sur la plante hôte habituelle. Les cycles évolutifs sont légèrement décalés et le vol des papillons plus tardif pour la forme de l'arolle.

Tout indique que nous avons affaire à deux races biologiques sympatriques dont l'étude est en cours. Peut-être s'agit-il d'espèces cryptiques comparables à *C. fumiferana* (Clem.) et *C. pinus* (Free). Le problème de la Tordeuse du mélèze présente ainsi un assez étroit parallélisme avec celui du "Spruce Budworm".

Je n'ai pu dans le cadre de ce bref exposé qu'esquisser le problème et présenter quelques résultats fragmentaires; attirer l'attention sur des recherches qui présentent de réelles difficultés en raison même de la biologie de l'insecte étudié et de la nature des forêts où elles doivent être conduites.

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### DISCUSSION

V. BUTOVITSCH. Prof. Bovey gave us a very interesting review of the larch tortrix and mentioned among other enemies of this moth a virus disease (granulosis). Has this virus been used for control work in Switzerland?

P. BOVEY. Un premier essai a été effectué en 1955, qui n'a pas donné de résultats, la maladie étant déjà répandue dans les populations par voie naturelle.



# Oak Defoliators in England

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## ABSTRACT

In a seven-year study of oak insects near Oxford, winter moth (*Operophtera brumata*) and green tortrix (*T. viridana*) have outnumbered all the other hundred species of caterpillars put together, but parasitism has not been high, and rarer species have often been parasitized by their specific parasites to a greater extent.

Sampling gives estimates of the population density and mortality of winter moth and of its parasites. The specific tachinid parasite *Cyzenis albicans* fails to increase even at a high host density. There is a heavy mortality of its puparia in the ground, and perhaps synchronisation difficulty. Specific ichneumon-fly parasites become adult soon after killing the host. Whether they are univoltine, or have an alternative host elsewhere, is unknown.

The percentage of green tortrix larvae parasitised is very low, but pupae are attacked by ichneumons which may be bivoltine and require alternative hosts.

The proportions of newly hatched larvae which fail to enter oak buds depends on the weather, but this is probably not the cause of differences in population density between species. The efficiency of specific parasites seems to be the major factor determining whether a species can reach destructive abundance or not, but the timing of outbreaks may be affected by the weather.

This work was begun in 1949 at Wytham (Berkshire) some 3 miles northwest of Oxford, with the help of a grant from the Agricultural Research Council, and has been continued since 1953 with the assistance of the Nature Conservancy.

The objective was to gain an idea of the role of parasites in the population dynamics of oak defoliators such as the winter moth (*Operophtera brumata* (L.)). The census methods devised for this study have provided also a lot of information about the population dynamics of over thirty other species whose larvae feed on the leaves of oak.

The winter moth larva feeds on a variety of tree species of which oak suffers defoliation most often. Quantitative sampling methods have been used on a small area containing some 20 oaks (*Quercus robur* (L.)) under which the undergrowth has been cleared. The area is near the edge of a large area of mixed woodland with thick under-scrub. Routine sampling has been confined to five trees within this small area since 1950.

The flightless females climb the tree trunks in November and December, and quantitative samples are collected with nets like lobster-pots fixed to the three trunks. The eggs are normally laid in crevices or under lichen high up the tree. A field test showed that at least 70% of the eggs laid survived and hatched in April 1956. Then the larvae seek to enter the opening buds.

Samples of foliage from the tree tops are used to estimate the population of lepidopterous larvae of all common species on the leaves. In some years larvae of the green tortrix, *Tortrix viridana* (L.), have been more numerous than those of the winter moth. The next most abundant species have been the spring usher, *Erannis leucophaearia* (Schiff.) and *Eucosma isertana* (F.), with other species even less common (Fig. 1).

Fully fed larvae of winter moth and many other species which pupate under the trees drop to the ground and the number falling per square meter is estimated by having two trays of  $\frac{1}{2}$  sq.m. area under each of the five trees. The trays contain water, and all the drowned larvae are identified, counted, examined and dissected for external and internal parasites. We now have estimates for eight consecutive years of the numbers of adult winter moth, of fully grown larvae, and of the percentage of parasitism.

To understand the interaction between the parasites and the winter moth we must also know the proportion of the parasites which survive in the ground to emerge



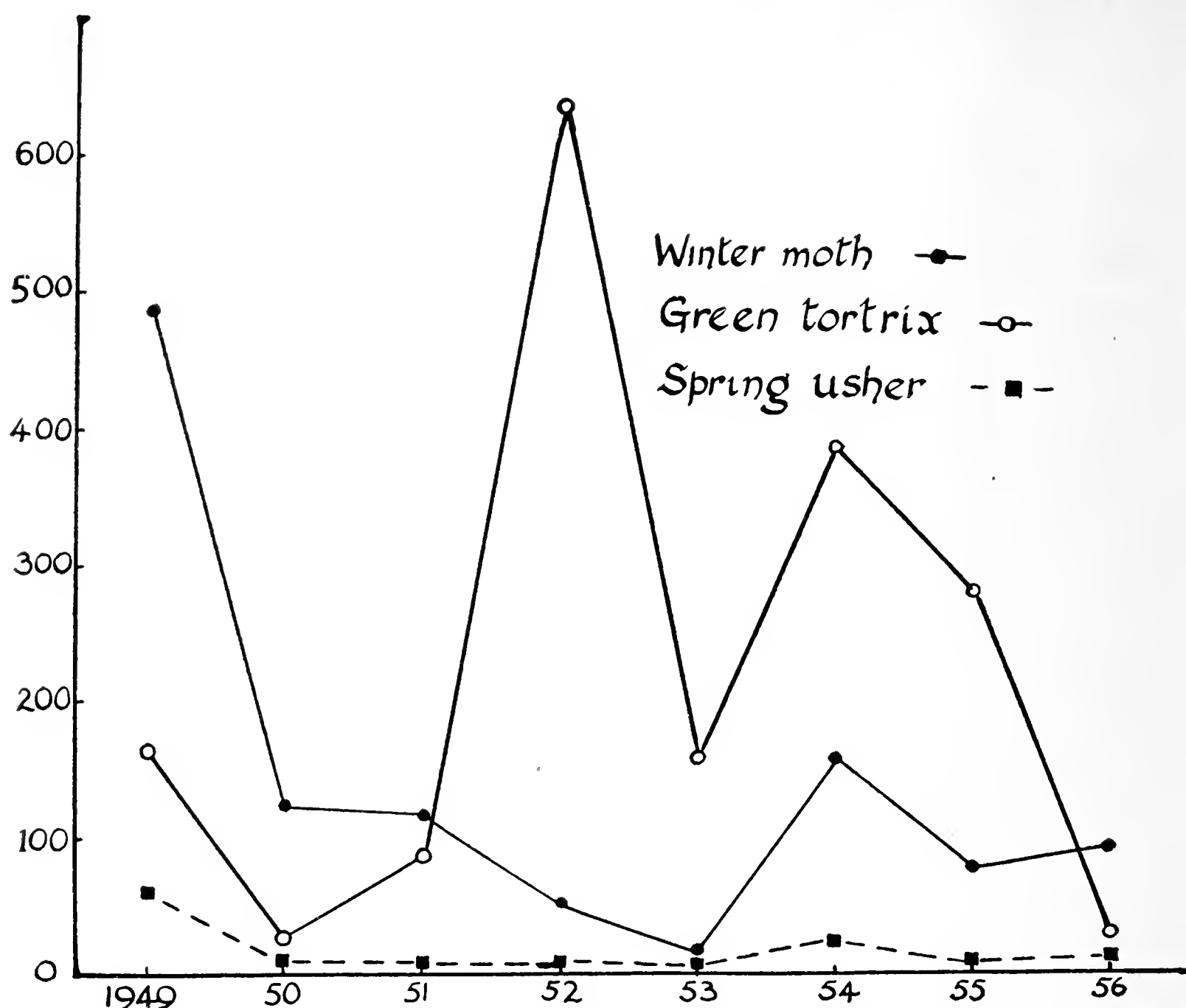


Fig. 1. Estimated number of larvae per square meter under oaks at Wytham.

as adult parasites in the next generation. This is found by putting traps over the ground from which the adult parasites emerge. Different species of parasites have different survival rates, but most are surprisingly low, often as low as 5%. Soil predators seem to be responsible for much of the mortality.

The winter moth census results show that the percentage of parasitism has not exceeded 30%. Only one of the common parasites, the tachinid fly *Cyzenis albicans* (Fall.), seems to have a life history synchronised with that of the host, and to be specific or almost so. This parasite has been introduced into Canada to control the winter moth. In England it is obviously ineffective. A study of its life history suggests the causes of this.

The flies emerge from their puparia in the winter moth cocoons in April, although no hosts are parasitised by them until mid June. In this long interval the flies are subject to predators, and the effects of any spells of inclement weather. Females in April have very small ovaries which contain no fully formed eggs and the flies probably require both protein and carbohydrate food to become mature, by which time the uterus may contain 2000 microtype eggs, many of which are pigmented and contain larvae ready to hatch. The source of food before the oak buds open is uncertain, but flies sunning themselves on tree trunks have been dissected, and the crop contained a yellowish fluid which gave a positive test with Fehling's Solution. This suggests the presence of reducing sugars with nectar as a possible food source, although no flies have been seen on the few flowers then present.

In June, flies have been found feeding on the sweet sap flux from young leaves damaged by caterpillars. H. G. Wylie in Canada had found that caged flies laid their eggs not in close proximity to suitable hosts on cut twigs, but on the honey pot provided to supply them with food. It is likely that in the field they oviposit on the margins

of the sweet sap fluxes, and that this ensures that eggs are close to a feeding larva. Whether they prefer to oviposit close to a winter moth larva rather than another species has not been tested.

If eggs are swallowed by a winter moth larva they hatch in the gut, and the minute maggots find their way into cells of the salivary (silk) gland of the host, where they grow slowly. The host larva continues feeding normally, and is killed after it has made a cocoon in the ground and pupated.

Although eggs of *Cyzenis albicans* are often swallowed by larvae of other Lepidoptera, they are able to develop in very few of them. Eggs have been fed to 16 species which have proved resistant to parasitism, and only on the congeneric birch-feeding *Operophtera fagata* (Scharf.) have puparia been produced.

Here then is a virtually specific and apparently synchronised parasite species with an egg production of about two thousand, whose host remains a common pest. Why is the parasite unsuccessful in controlling the host population at a low level?

1. The survival of *Cyzenis* eggs laid on the leaves depends on the proportion of leaves eaten by winter moth. Egg survival is probably low, unless the trees are almost defoliated by winter moth.

2. The puparia of *Cyzenis* are in the ground from July until April, and the proportion which emerge as flies may be as low as 4%. The rest are probably destroyed by soil predators.

3. The adults flies themselves are in danger from predators such as spiders and birds for more than 2 months.

4. Flies with full uterus have been found when most winter moth larvae had ceased feeding. Synchronisation of parasite and host is thus imperfect.

As a result of a combination of these factors, the population density of *Cyzenis* fell by 1953 to under one hundredth of the 1949 figure.

The other parasites of winter moth which we find attacking no other host on oak are species which become adult soon after killing the host larva. Thus the Hymenoptera, *Rogas testaceus* (Spin.) and *Lissonota femorata* (Holm.), kill a small percentage of winter moth larvae, and become adult in July of the same year. They possibly then attack some other host, but if so, this is not on oak. Such parasites may perhaps be effective controlling agents of the unknown alternate host, but they are ineffective against winter moth.

Green tortrix has been more abundant than winter moth in the more recent years of the census until 1956. The percentage of larvae parasitised is seldom more than 5%, and all the species of parasites concerned emerge as adults by July, and either require alternative hosts then or perhaps enter diapause and hibernate. In contrast the pupae of green tortrix and those of the many other tortricids are frequently attacked by a series of ubiquitous pupal parasites, such as the Pimplines, *Itoplectis maculator* (F.), *Apechthis rufata* (Gm.), *A. resinator* (Thunb.) and the Ichneumonine, *Phaeogenes stimulator* (Grav.) (= *invisor* Thunb.). These too seem to have no hosts available on oak which are suitable for a second generation, and the lack of a diapause which might permit synchronisation with the host seems to be a bar to their effectiveness.

Oak trees vary greatly in their susceptibility to defoliation. Each year the trees flush in a similar order, although the actual date varies considerably from year to year. Those trees whose buds open earliest suffer most severely, and the late trees whose buds open perhaps ten days later suffer less damage. This is because the winter moth eggs hatch near to the time that the buds begin to open. When the young larvae fail to enter firmly closed buds, they drop off on silken threads and may then be blown considerable distances. Many perish at this stage, but the proportion of the young larvae surviving on the early flushing trees may be five times as high as on the late flushers (Table I). As a result the population density of larvae falling to pupate under early trees is much higher than under late trees. This is partly compensated by a differential pupal mortality (perhaps due to predators) which may give rise to pupal survival under late trees being as high as three times that under early trees (Table I).

TABLE I.  
Effect of Time of Oak Bud Opening on Winter Moth Survival 1952.

Trees arranged in order of leaf opening					
	earliest at left,			latest at right.	
	5	9	1	15	8
Eggs per sq.m.	1270	1330	1480	1220	1030
% enter buds	9.5	4.8	2.9	2.4	1.9
larvae per sq.m.	120	63	43	29	19
% pupae survive	9.9	9.6	9.5	17.7	27.2
adults per sq.m.	12	6	4	5	5

Winter moth and green tortrix are pests apparently because their parasites are ineffective. These pests suffer the greatest proportionate loss in the first larval stage. Survival at this stage is very variable from year to year, probably owing to weather factors. These differences go far to explain the big changes in population density, which are often synchronous over a wide area.

# The Population Dynamics of the Spruce Budworm in Eastern Canada<sup>1</sup>

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## ABSTRACT

The spruce budworm is the most destructive defoliator in eastern Canada and intensive studies on its population dynamics have been in progress for ten years on the Green River Watershed in northern New Brunswick. Life tables are developed for successive generations of the budworm in different types of forest stands and this paper presents the conclusions reached through the analysis of a large series of life tables. The important sources of mortality are related to stand factors, population density, and/or climate. Because of the high dispersal losses suffered by early-instar larvae and by moths, stand factors are the essential predisposing cause of outbreaks and outbreaks do not develop where the forest is sufficiently discontinuous or variable. Parasites respond to host density, in a delayed manner, and are capable of exerting control in stands where the increase in population is not too rapid or sustained; but in stands that are favourable to rapid population development, parasites suffer some limitation that is not yet understood and appear incapable of overtaking the host. Also, the transport of gravid moths by turbulent winds is related to topography and can destroy the synchronization in space between the budworm and its enemies. When stand factors are favourable, climatic cycles determine the general incidence of budworm outbreaks in time and place.

## INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is by far the most destructive defoliator in Canada and its periodic outbreaks constitute major forest disturbances. Like a number of other important insects, the spruce budworm is poorly named. Balsam fir, *Abies balsamea* (L.) Mill., rather than spruce, is the host that encourages the outbreaks and suffers the greatest damage. The budworm is native to North America and does not occur elsewhere. In New Brunswick the history of budworm damage has been traced back as far as 1770 and outbreaks have occurred at intervals of 35-40 years. No doubt many earlier outbreaks occurred for they seem to be a part of the natural cycle of events associated with the maturing of extensive forests of balsam fir.

In 1945 a long-term project was initiated on the Green River Watershed in northern New Brunswick for the study of the population dynamics of the budworm in relation to forest types and silvicultural treatment. Over the past ten years a group of biologists has been assembled to investigate different aspects of the population dynamics of the budworm and of associated insects on balsam fir. The authors are respectively concerned with integration and sampling design, parasitism, bioclimatology, and extensive surveys of infestation and damage in relation to forest conditions. Although other aspects of the project will not be treated in any detail in the present paper, we wish to acknowledge the co-operation of other members of the group, especially M. M. Neilson (budworm diseases and constitutional factors) and W. F. Cheshire (vertebrate predators of the budworm). All these lines of investigation overlap in many ways and collaboration is very close. Most of the field data are gathered by joint effort and the work is designed to permit results to be brought together in the form of life tables.

The object of this paper is to describe rather briefly what appear to be the major factors in the population dynamics of the spruce budworm. This will be based largely on the Green River studies but the results of recent work in Ontario will also be used, as well as the rather sketchy information available on earlier outbreaks. For more adequate citations to the studies in other parts of Canada, you are referred to a recent review of the budworm by Prebble (1954).

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## MATERIALS AND METHODS

The approach used in the Green River studies is the development of life tables for each succeeding generation of the budworm in different types of forest stands. A description of this technique with examples of life tables has already been published (Morris and Miller, 1954), as has also the design of the detailed population sampling which provides the basic reference points in the life tables (Morris, 1955). The techniques for the study of parasitism (Miller, 1955), fecundity (Miller, 1957), climatology (Greenbank, 1956), moth dispersal (Greenbank, 1957), and other aspects of the work have recently been published in the Canadian Journal of Zoology, or will be published shortly, so it is not necessary to discuss methods here in any detail.

If we include the 1956 season, about seventy life tables have been completed. They cover several forest conditions including extensive, overmature balsam stands in the centre of the outbreak, young stands, and relatively isolated stands in areas under operation for pulpwood. The tables also apply to three rather distinct levels of population, which will be designated here as *endemic*, *epidemic*, and *intermediate*. When the work was started in 1945 population was very low over the entire area and did not increase significantly until 1947. The populations studied in the first two years may represent the endemic condition that persists between outbreaks, but there is no assurance that some increase over this condition did not occur before 1945. Our data on the endemic condition are therefore inadequate and can be strengthened only by extending the work well beyond the present outbreak period. The epidemic condition is well represented in our series of life tables for a thirty square-mile check area that has been reserved from both cutting and spraying operations. Population reached a peak on this area in 1951 and has since been declining as a result of foliage depletion. Tree mortality is well advanced and will soon approach 100 per cent in some stands. The intermediate condition, which is also well represented, applies to the fluctuating population in certain stands where conditions have not favoured an increase to the epidemic level. Although these populations have remained above the endemic level, they have not gone high enough to cause serious defoliation.

The conclusions to be presented here are based on the examination and comparison of all the life tables, with particular attention to mortalities that vary significantly with time or place. A number of factors give rise to mortality that is relatively constant from year to year and from stand to stand. Although the contribution of these factors to total mortality cannot be ignored, they play a minor role in population dynamics and, in the interests of brevity, will not be discussed here. Other factors cause variable mortality that is clearly related to forest conditions, to population density, or to climate, and only these factors will be discussed. Also, this is a preview of results rather than a detailed presentation and you may wish to accept the conclusions with reservations until statistical analyses are published.

## THE RELATED MORTALITY FACTORS

For want of a better term, the factors to be discussed here will be called "related" mortality factors, indicating that the degree of mortality is related to stand factors, to population density, or to climate. Fig. 1 will be used throughout in explaining these relationships.

**LARVAL DISPERSAL:** The eggs are laid in late July and early August. The tiny first-instar larvae emerge in August and have only a few hours of activity before they form hibernacula on the tree. During this period of wandering many drop from the foliage on silken threads and are transported very readily by wind or convectional currents. After drifting many are deposited on unfavourable hosts or in other places where they cannot survive. They have been observed in large numbers, for example, on lakes. The larvae not lost during dispersal spin hibernacula and moult to the second instar without feeding. More than three-quarters of the life cycle is then passed in hibernation, a period in which mortality is rather consistently low and appears to have little relation to climate or other external influences. In May of the following year the tiny larvae are again subject to high dispersal losses as they leave the hibernacula and move to feeding sites. For simplicity, we propose to group these two dispersal



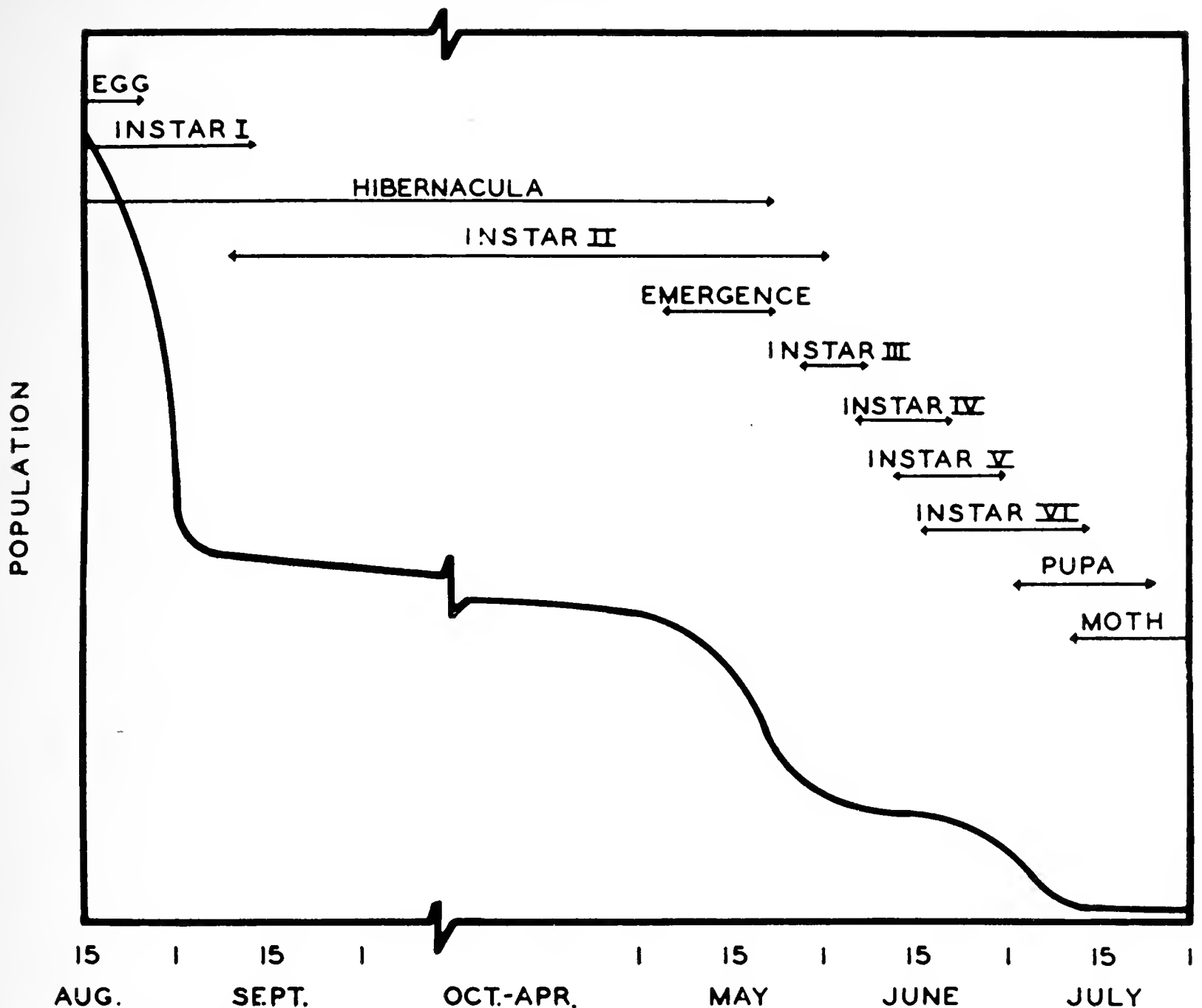


Fig. 1. Typical survivorship curve during one generation of the spruce budworm.

periods (August and May, Fig. 1) and refer to this source of mortality as larval dispersal. As other factors are also involved, this represents an over-simplification but it will be useful for present purposes.

Population measurements on the same trees before and after these periods provide a measure of dispersal loss for use in life tables, and this loss is clearly related to the density of balsam fir and to the relative continuity of the forest. In typical mature balsam stands on the Green River Watershed, mortality through larval dispersal averages 80%; in extremely dense balsam stands it may be as low as 60%; in mixed-wood stands and in relatively small stands of balsam isolated by clear-cutting it may exceed 90%. Some of our best examples come from stands that were purposely isolated. The trees in the middle of a 5-acre plot, for example, showed a loss of 76% while the plot was part of a continuous forest; when the plot was isolated on all sides by clear-cutting, the loss increased to 93%. Mortality in dispersal periods also seems to increase as trees are killed by defoliation and stand density is lowered.

Our data suggest that larval dispersal is a rather local phenomenon and that dispersal loss is remarkably consistent from year to year in a given type of stand. Theoretically, air-borne larvae could be carried great distances and provide a source of infestation for other stands, but in this respect larval dispersal is not as important as moth dispersal. We have never recorded gains in population after larval dispersal. Larval emergence in both August and May continues over a period of ten to twenty days and each larva is subject to dispersal only during its active period of a few hours. Thus large segments of the population are not likely to be transferred systematically from one place to another. In the moth stage, on the other hand, a large proportion of the population may be available for transport at any one time.

**LARVAL PARASITES:** The principal parasites of the budworm cause larval mortality in the later instars and are partly responsible for the dip in the survivorship curve

occurring in late June and early July (Fig. 1). As will be shown later, parasitism is related in a delayed manner to the population density of budworm larvae. At Green River we have seldom found larval parasitism over 40% and a review of parasite data from other parts of Canada (Prebble, 1954) suggests that this limit is not frequently exceeded. It should not be concluded, however, that parasites are unimportant. The life tables show that with the average larval dispersal loss of 80%, and with mean values of the various "unrelated" mortality factors, a larval parasitism of 40% is sufficient to prevent a population increase. In less favourable stands, where larval dispersal gives a 90% loss, a parasitism of 30% would be sufficient to prevent increase if other factors remained the same; and where the dispersal loss is 95%, a parasitism of 10% would be sufficient. Small increases in dispersal mortality, therefore, have a very important influence on the degree of mortality that must follow in order to prevent population increase. As parasitism is nearly always higher than 10%, it is clear that budworm populations are not likely to increase under forest conditions that give high dispersal losses.

**LARVAL COMPETITION:** Under epidemic conditions competition for food is an important factor that is related to population density. Mortality results both from starvation and from the associated wandering and dropping from the trees in the later larval instars.

**OTHER FACTORS AFFECTING LARVAE AND PUPAE:** Other factors contribute to the rapid population decline in late June and early July (Fig. 1) but it is not yet clear whether they may properly be classified as "related" factors. For example, the series of life tables suggest that larval mortality is increased when weather prolongs development, but so far the differences in mortality between favourable and unfavourable years are too small to show statistical significance (Greenbank 1956).

The budworm is attacked by viruses, protozoa, and fungi but these disease organisms appear to be consistently low in virulence. The Green River work to date suggests no clear relationship between the incidence of disease and either population density or weather conditions.

Various species of birds, small mammals, and invertebrate predators also attack the budworm and some interesting changes in the species composition of wood warblers occur during budworm outbreaks. In general, however, the populations of predators do not respond in a significant way to increases in budworm population. Thus, population studies on predators in relation to budworm populations show that they are incapable of exercising important control under the epidemic conditions that have prevailed in recent years. Under endemic conditions they may be more effective, especially if their feeding habits are such that predation is related to budworm population over a certain range in density. Continuing studies on their populations and feeding habits will be an important part of our post-outbreak program.

**REDUCED FECUNDITY:** The survivorship curve (Fig. 1) shows two moths surviving (one male and one female) from an initial population of 200 eggs. This represents a generation mortality of 99% and ensures a constant population level under ideal conditions where the average female can lay 200 eggs. By using the mean size of emerged female pupae (Miller, 1957) we have detected one or two field populations that closely approached this figure. Lower figures are more common, however, because fecundity is related to stand factors, particularly flower production, to weather, and to population density. Ideal conditions occur when there is an abundant production of staminate flowers on balsam fir, for they represent both a preferred food for early-instar larvae and a microclimate that considerably speeds development (Blais, 1952). Ideal conditions also occur when climate favours rapid larval development in relation to shoot development. The larvae feed by preference on the new shoots and larvae whose development is delayed until late in the period of shoot growth give rise to adults with reduced fecundity (Greenbank, 1956). In outbreaks the fecundity of the budworm decreases progressively each year in response to the reduction in both quantity and quality of the food. In a stand that has suffered five or six years of severe defoliation, mean fecundity may be reduced to 75 eggs per female in place of 200 (Miller, 1957).

To date, however, there is no clear evidence of an accompanying hereditary weakness, as proposed by Franz (1949) for certain defoliators in Germany.

**MOTH DISPERSAL:** Moth dispersal is the most dramatic, if not the most important, of the whole group of related mortality factors. Like fecundity, it is related to weather processes, to stand factors, and to population density. The effects of weather processes give rise to two types of moth dispersal (Greenbank, 1957): (1) Convectional transport, in which large numbers of moths are borne aloft and may be carried many miles by the updraughts associated with the passage of cold fronts. This type of transport is generally responsible for the tremendous flights of moths that have descended on various Canadian cities, sometimes when the nearest budworm infestation was 50 miles away. (2) Turbulent wind transport, which is a more local phenomenon similar to larval dispersal. Moths transported by either method are often predominantly females retaining a proportion of their egg complement (Greenbank, 1957); thus moth dispersal can play a major role in the population dynamics of the budworm in a given stand. This is clearly revealed in life tables by comparing actual egg population in a stand with the egg population expected from the supply of emerged female pupae. Such comparisons sometimes show significant gains or losses in population that can be explained by no other factor, and this is supported by light-trap records, by the appearance of flights in towns and cities, and by the rapid re-infestation of large sprayed areas.

The relation of moth dispersal to stand factors and to population density is also quite apparent. Through the action of turbulent wind, moths are frequently dissipated from isolated or low-density stands. This is a similar process to the dissipation of small larvae, and the bodies of moths have also been observed in large numbers on lakes. Good illustrations of this type of loss are again available through the development of life tables for stands isolated by cutting operations. For example, a plot which originally supported a high budworm population lost 88% of its moth population in the year of isolation and 95% the next year. Similarly, when cutting operations pass through a severely infested stand, the residual, scattered trees are unable to maintain their budworm population. For reasons not fully understood, young stands tend to lose more moths than neighbouring mature stands, the ratio of egg to pupal populations being consistently lower in young stands until the mature stands have suffered severe defoliation (Miller, 1957). Stands that have suffered severe defoliation for several consecutive years lose a large proportion of their moths, so dispersal is at least indirectly related to population density. Again, the reasons are not clear but it is suspected that the scarcity of the preferred oviposition sites on new or recent foliage keeps the females more active and hence more likely to be carried away by air currents.

In some situations, then, moth dispersal acts as a mortality factor. It can also act the other way and we have a number of instances where population has been increased through moth influx. Budworm populations showed gradual increases over the Green River Watershed at least as early as 1947, but there is evidence that the outbreak was hastened in some parts of the Watershed by a large-scale moth invasion in 1949 (Greenbank 1957). Convectional transport from infestations to the west was involved to some extent, but wind dispersal of local populations can have the same results. Extensive surveys of budworm infestations in New Brunswick and eastern Quebec showed that defoliation tended to appear first on the upper slopes. It is logical to assume that local topography favours some areas for moth deposition and others for drainage. The concentration of population in areas of deposition can provide such rapid increase that natural enemies are rapidly outdistanced. Relationships of this type can be recognized only in the early stages of the development of an outbreak or in peripheral areas; in later stages, as a result of the great momentum achieved in favourable areas, isolated stands, young trees, and all topographic sites may become severely infested.

## THE MAJOR INFLUENCES IN POPULATION DYNAMICS

From the discussion of mortality factors, it is concluded that four major influences determine budworm numbers at a given time: stand factors, climatic variations, natural

enemies (particularly parasites), and foliage depletion. They are discussed further below and illustrated by Figs. 2, 3, and 4.

**STAND FACTORS:** The density and continuity of balsam fir are the important stand factors because they determine to a large extent the magnitude of the dispersal losses suffered by larvae and moths. The age of the fir is also of importance because density, or foliage quantity per acre, increases with age; because flower production increases with age; and because moths tend to oviposit in the tallest trees. From this we should expect budworm outbreaks to develop and gain their momentum in extensive areas of mature fir, and the fact that they do so only in such areas has been referred to very frequently in the literature (Prebble and Morris, 1951). In short, in order to have an outbreak of the budworm we must first have an "outbreak" of balsam fir.

By way of illustration, an attempt has been made to re-construct the course of events in the development of a typical mature balsam stand on the Green River Watershed (Fig. 2). This stand originated in the 1870's, perhaps through the destruction of the parent stand by the Saxby Gale of 1869. The density of foliage per acre (Fig. 2, B) increased with the age of the stand to a maximum at about 55-60 years, and then started to decline as trees were removed through the action of decay and wind. Flower production (Fig. 2, C) began at age 25 and reached its peak considerably later than foliage production, for it depends both on age and exposure to light (Morris, 1951). The most favourable conditions for the budworm therefore occur in mature or over-mature stands. This stand was too young to show any effects from the outbreak of 1878 (Fig. 2, A), which killed some older stands in other parts of northern New Brunswick; the slight hump in population is shown merely to suggest that some moths from older stands may have been blown into the area. The outbreak of 1912 also did its greatest damage in older stands nearby, which originated in 1850. However, defoliation was very severe for several consecutive years in the stand illustrated, which was then 35-40 years old; some trees were killed (dip in Fig. 2, B); flower production was interrupted through the destruction of the shoots (Fig. 2, C); and ring growth was reduced very conspicuously. In general, however, stands of this age-class survived, partly because they suffered their first severe defoliation about two years later than did older stands in the immediate vicinity (as indicated by present studies in stands of different ages), and partly, no doubt, because of the greater resistance of young, vigorous trees. A few decades later, however, this stand was both extremely favourable to population development and very vulnerable to damage. The great reduction in shoot growth associated with heavy flower production is among the factors favouring complete loss of new growth (Morris, 1951). Thus, in the present outbreak, defoliation of new growth became severe in 1950, trees started to die in 1954, and tree mortality will be almost complete in another two or three years.

Very little is known about the population behaviour of the budworm between these three outbreaks (Fig. 2, A). It is probable, however, that the population fluctuates at a very low level relative to the outbreak level. Extensive forest insect survey work in New Brunswick between 1938 and 1944, prior to the present outbreak, yielded very few specimens of the spruce budworm, although it should be mentioned that the collection methods and the type of trees sampled were not very well adapted to this insect. In any event, however, it is clear that budworm population does not respond directly to foliage quantity (Fig. 2, A, B) and that other factors can hold populations at a low level even during periods when the concentration of foliage and flowers is favourable. Stand factors, therefore, should not be considered as immediate regulating factors on population density but rather as pre-disposing factors that are essential before outbreaks can occur. The illustration described here applies to conditions in a large, continuous stand of nearly pure balsam; in isolated or mixedwood stands, population behaviour may be quite different (cf. Fig. 3).

**CLIMATIC VARIATIONS:** Using a synoptic approach to studies of spruce budworm outbreaks in central Canada in relation to climatic variations, Wellington (1952) has shown that the three- to four-year period preceding each budworm outbreak was characterized by southward shifts in the circulation pattern. These shifts permit polar air to predominate over the affected areas and this is attended by reduced precipitation



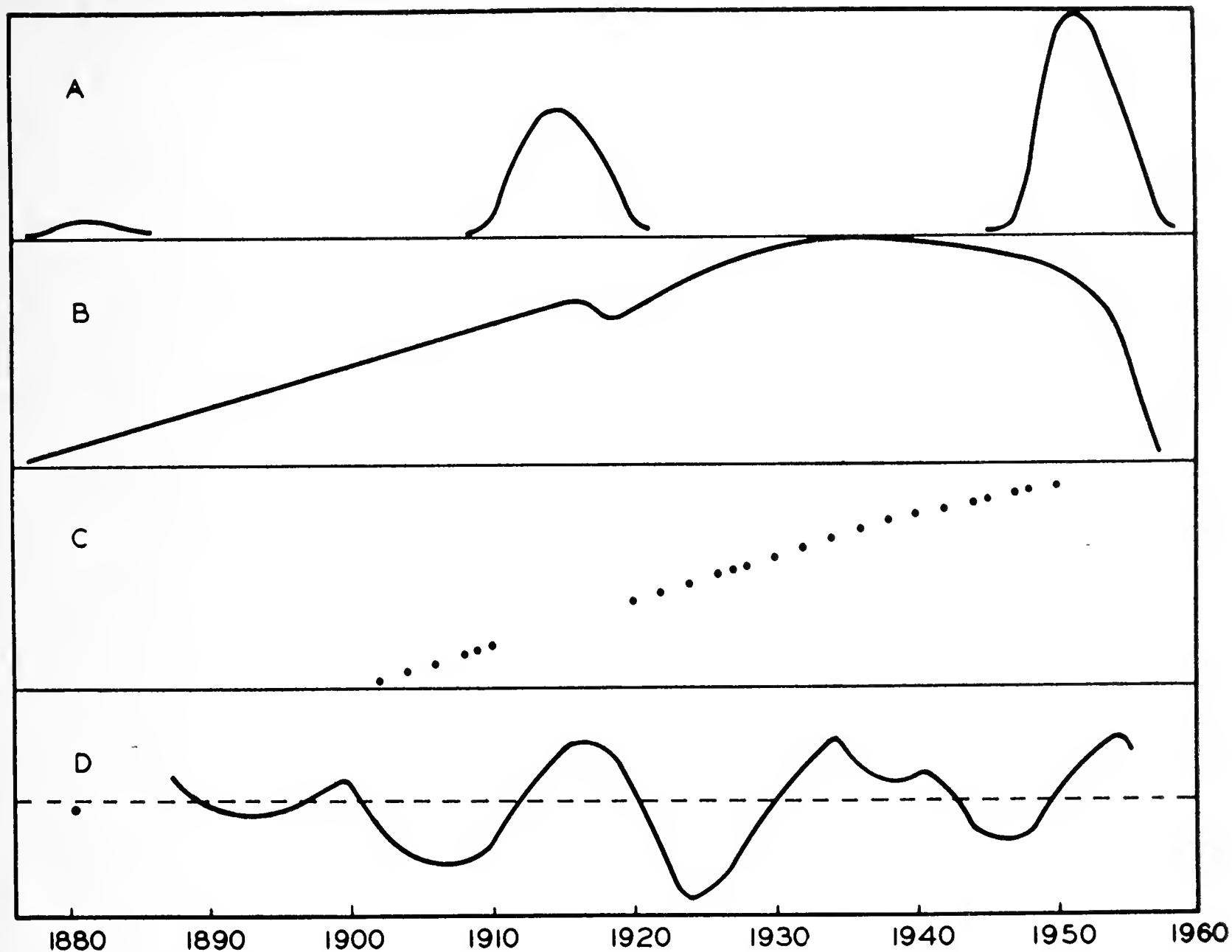


Fig. 2. Spruce budworm outbreaks in relation to the development of a typical balsam fir stand on the Green River Watershed.

A: Budworm populations per acre expressed as common logarithms. Population behaviour during endemic periods is not known, while in the outbreaks of 1878 and 1912 it is based largely on the effect of defoliation on the radial growth of surviving trees.

B: Foliage density based on the assessment of branch surface per acre in existing stands of different ages (Morris, 1955).

C: Staminate flower density, with dots representing flowering years, based on the study of flowering history (Morris, 1951).

D: Deviations from normal June rainfall, smoothed by running averages (Greenbank, 1956).

and by the dry, clear conditions most suitable for budworm development. Greenbank (1956) has obtained supporting information for the New Brunswick outbreaks. Thus, using June rainfall as an index of general weather, since June is the month in which most of the larval development takes place, we see that both outbreaks of the present century developed during dry periods (Fig. 2, D). The concept of "climatic release" helps to explain in definite terms the incidence of budworm outbreaks in time and place. The mechanism through which it operates is not fully understood, but apparently the effects of climate are relatively indirect. The budworm is well adjusted to extremes in Canadian climate and direct mortality attributable to meteorological extremes is only rarely observed. We have already mentioned that rapid larval development in relation to shoot development increases fecundity, and this increase may be further emphasized by the effect of dry cycles on flower production. Balsam fir normally flowers in alternate years but under suitable weather conditions it may flower in consecutive years (Fig. 2, C). It is also possible that climate may affect the synchronization between the budworm and its parasites, or increase the period of exposure to vertebrate enemies. In any case, its main effects seem to occur at the endemic level; once population is released from this level it is capable of further increases, despite unfavourable weather (cf. Fig. 2, A, D) and the outbreak generally continues until the foliage supply is depleted. Also, climatic release does not lead to serious outbreaks unless the predisposing stand factors



are suitable. The severe drought of the 1920's (Fig. 2, D) did not cause a budworm outbreak in New Brunswick, presumably because the most favourable stands were destroyed in the widespread outbreak that preceded it.

**NATURAL ENEMIES:** The present discussion of natural enemies will be limited to parasites, using Figures 3 and 4 as illustrations.

Under the endemic, or near-endemic, conditions of 1945 and 1946 two species of larval parasites were common, at least one of them being a general parasite that has been recorded from a number of tortricid hosts. With the first host increase in 1947 these species became scarce relative to the budworm and since 1949 neither has been recorded in Green River populations. Three different species, barely recorded in 1945 and 1946, became more common in 1947 and have remained the three most prevalent species during the outbreak period. Their behaviour to date in relation to host population has been rather similar so for simplicity we shall use only one — *Apanteles fumiferanae* (Vier.)—for illustration. This is a specific, univoltine parasite that attacks the over-

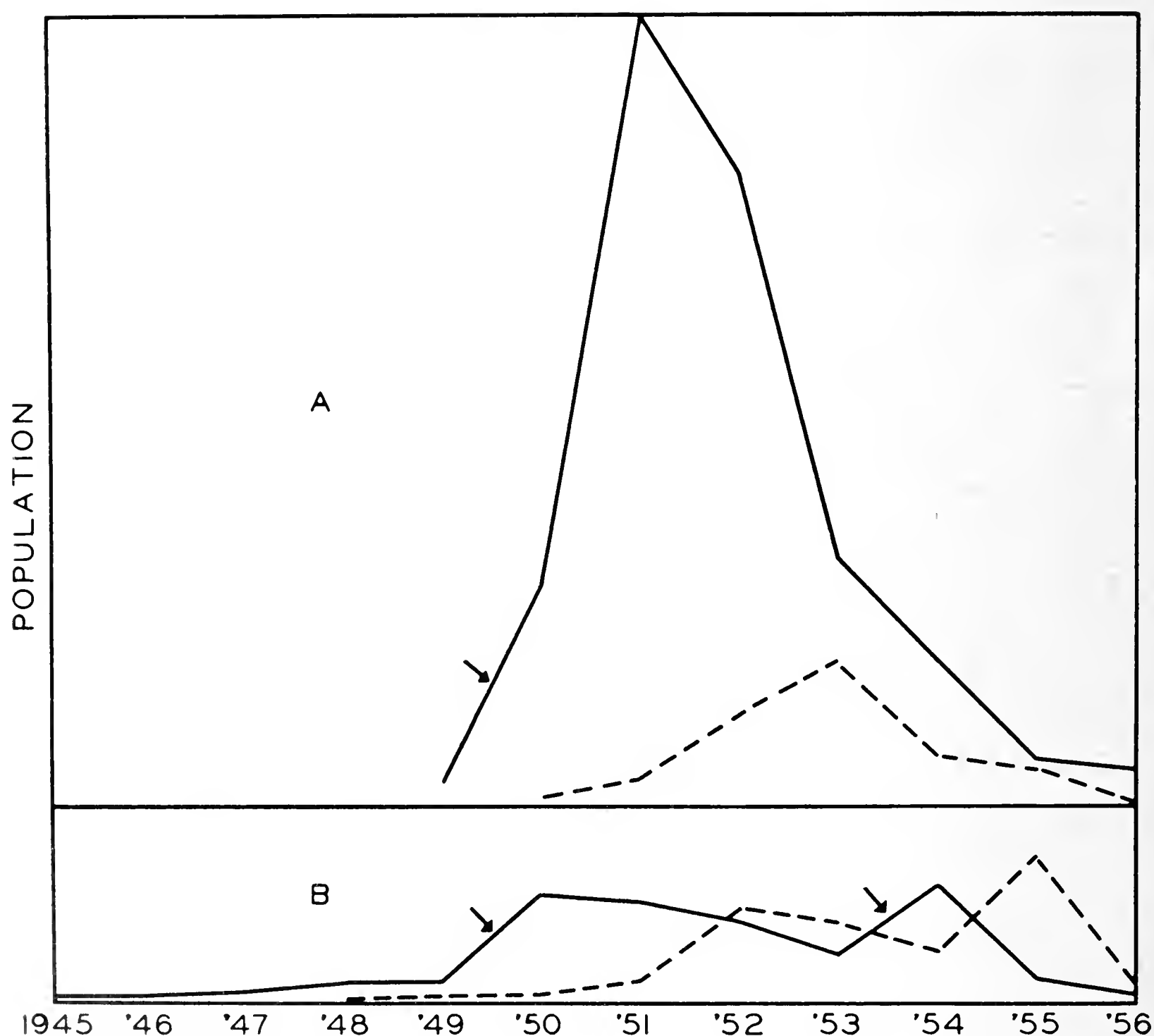


Fig. 3. Annual host density in relation to parasite density on two study plots on the Green River Watershed. The methods used in securing the parasite data are described by Miller (1955).

A: Plot in severe infestation, where severe loss of new foliage occurred by 1950 and trees started to die by 1954. Populations prior to 1950 are believed to be the same as in "B".

B: Plot in more isolated stand, a few miles from "A", where defoliation has never become severe. Solid lines: Population of spruce budworm larvae available for attack by parasites. Broken lines: Population of adult *Apanteles fumiferanae* (Vier.) available to attack spruce budworm larvae. The scales for host and parasite populations are different, but when the broken line is above the solid line it may be taken that the parasite (when added to the other mortality factors) is capable of controlling the host. Arrows: Influx of spruce budworm moths.

wintering host larva in August and remains in the host until the following summer. Multiple parasitism of spruce budworm larvae is rare.

In one plot (Fig. 3, B) there was a sharp rise in host population in 1950, largely as a result of moth invasion in 1949, but the isolated nature of the stand did not encourage rapid multiplication of the invaders. Thus, in the next two years, the parasite was able to increase to a point where parasitism, when added to other mortalities, was sufficient to cause a decline in host population. After 1952, one would expect a continued decline to a low level but a further moth invasion gave an unexpected increase in host population in 1954. Thus the maintenance of a moderate budworm population on this plot has been largely the result of moth influx from severe infestations nearby. The parasite has responded, in a delayed manner, to these increases in host population and appears capable of controlling the host once the source of re-infestation is removed. Other stands unsuitable to rapid budworm multiplication have shown similar population behaviour, except that in some cases only one invasion occurred.

In the area of severe infestation (Fig. 3, A) the picture is quite different. The host increase of 1950 was much greater and probably resulted from both influx and local multiplication in 1949. This was followed by another rapid increase in 1951. The parasite responded at a rather slow rate until 1953 and if it had continued to respond it would have overtaken the host by 1954, in time to prevent much of the tree mortality. However, in severe infestations of the spruce budworm parasites have certain limitations to their behaviour which are not yet understood. These limitations are apparent in Figure 4, where the number of hosts attacked per adult parasite is shown to

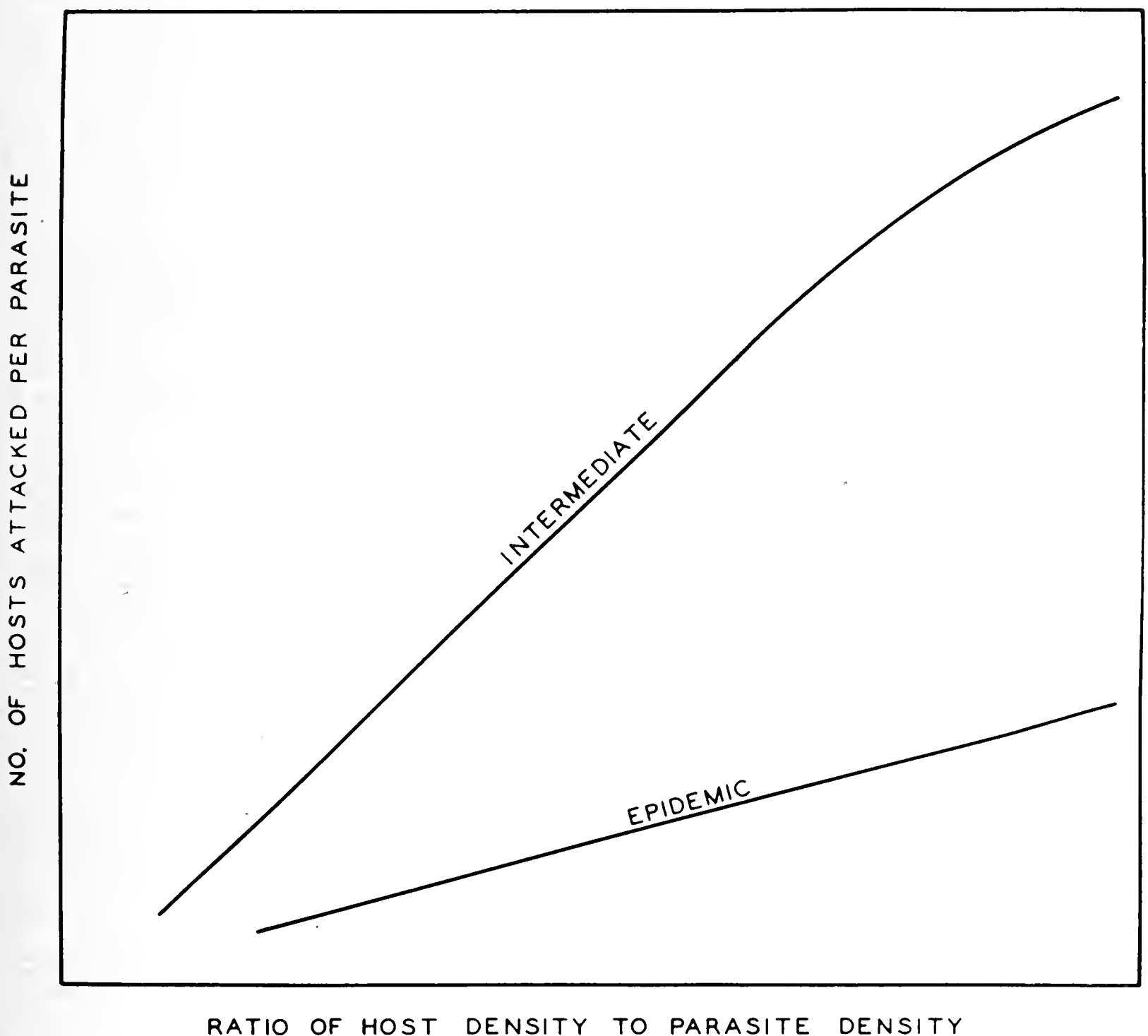


Fig. 4. Behaviour of *Apanteles fumiferanae* (Vier.) in intermediate populations of the spruce budworm as contrasted to its behaviour in epidemic populations. Based largely on data collected between 1951 and 1956 from several plots in each condition, including the plots shown in Fig. 3.

be considerably reduced in areas of severe infestation. Percentage parasitism by this one species has reached 26% in areas of intermediate population but has remained below 10% in outbreak areas. Hypotheses to explain this difference in behaviour are now being tested but as they are still rather speculative they will not be discussed here.

In brief, then, our studies of spruce budworm parasites suggest that the complex of prevalent parasites may be rather different under endemic and epidemic host populations; that parasites may exert effective control where host population does not increase too rapidly; and that the behaviour of a parasite in severe infestations is limited by factors other than host density.

**FOLIAGE DEPLETION:** Foliage depletion resulting from budworm feeding is the factor that limits and suppresses populations in severe outbreaks. The budworm feeds largely on new shoots and about five successive years of this type of defoliation are required to kill balsam fir. Before mortality occurs, however, the ability of the tree to produce a full complement of new foliage each year is seriously impaired. In 1951, the budworm population greatly overshot the supply of new shoots (Fig. 3, A), and the decline in population after that year is largely attributable to the depletion of foliage. Several types of population loss are involved including direct starvation, loss in fecundity, and particularly the increased dispersal loss of female moths from severely defoliated stands.

### NATURAL CONTROL

A theory covering the natural control of the spruce budworm under all conditions of population cannot be advanced until the endemic condition has been more thoroughly studied. We know, however, that the upper limit of numbers is controlled only by the foliage supply and that the suppression of numbers during outbreaks is accomplished largely by foliage depletion. However, after an extensive forest of mature balsam has been destroyed by an outbreak or by other factors, there is a long period during which control is assumed by other factors. Whether numbers simply vary during this period, due to the random action of the whole control complex (Cole, 1954), or whether they are regulated by density-related processes (Nicholson, 1954) is not yet known. In view of the importance of climatic release, however, we might expect population to respond to favourable years, but as dispersal losses in young or diversified forests are very high, increased numbers are no doubt rapidly dissipated. Also, when increases are not too rapid or sustained, natural enemies may be capable of reversing a rising trend. We have seen that such enemies as parasites are able to overtake the budworm under such conditions. But whatever type of control may operate during this long endemic period, the situation becomes very precarious as the forest ages and the concentration of foliage and flowers increases. Once stand factors become favourable, it requires only three or four consecutive years of favourable climatic conditions to release the budworm from its endemic control factors. This release may be aided by moth invasion from existing outbreaks to the west, particularly in areas like New Brunswick, but this is not essential. It may also be aided by the effects of topographic features on airflow during moth dispersal, which tend to concentrate populations in certain locations.

Thus the work on the spruce budworm to date lends support to what Solomon (1949) has termed a "comprehensive" theory of natural control. None of the more specific theories is capable of providing a satisfactory explanation of the population dynamics of the spruce budworm. Some support of Nicholson's (1933, 1954) ideas on density relationships has been demonstrated, with regard to both the food supply and the action of parasites. However, restriction of our attention to these relationships would provide little of value in explaining the incidence of outbreaks in either place or time; furthermore, his cavalier treatment of edaphic influences is in strong contrast to the importance of these influences in the population dynamics of the budworm. Thompson (1939) believes that discontinuity and variability in habitats is the primary extrinsic factor of natural control, and this idea is also supported since destructive budworm outbreaks do not develop where the forest is essentially discontinuous and diversified. In the case of this insect, dispersal is largely an involuntary process, however, and although the loss increases with the severe defoliation resulting from population pressure, it does not depend upon it. Also, although stand factors represent an essential predisposing cause

of outbreaks, they do not represent an immediate cause. Climate is the factor that determines, in the immediate sense, the time and place of rapid population growth. The budworm also offers some support, therefore, to the climatic school of population theorists and is discussed by Andrewartha and Birch (1954) as an example of a natural population "in which the numbers are determined largely by weather." Besides some obvious errors concerning such important factors as the host trees, their treatment of this insect is incomplete, however, and ignores the other major influences in its population dynamics. In short, it appears that any satisfactory theory on the natural control of the spruce budworm will have to give equal attention to biotic, edaphic, and physical factors.

These remarks apply only to the spruce budworm and not necessarily to forest insects in general. The budworm is an unusual insect, for the great majority of defoliators on the same host tree never erupt to the point of depleting their food supply; further, our studies to date apply largely to an epidemic population of the budworm, which represents a more unusual condition than an endemic population. By extending the studies on the budworm and its associated defoliators well into the post-outbreak period we hope to learn what factors determine the endemic level and wherein they periodically fail for the spruce budworm but not for other species. Does the spruce budworm lack efficient parasites? *Acleris variana* Fern., an associated tortricid on fir, becomes numerous enough at Green River to cause conspicuous defoliation but is overtaken by its parasites before any tree mortality occurs. Or is the budworm's great susceptibility to dispersal the thing that makes it different from other defoliators? Few other insects except locusts have appeared so conspicuously in mass flights.

### CULTURAL CONTROL

Applied control measures are scarcely within the scope of the present paper. However, since the fundamental, long-term control of the spruce budworm would appear to be largely a matter of taking advantage of natural control, a brief reference to this subject may not constitute a serious digression.

After the first outbreak of the present century, observations on the pattern of damage in relation to forest conditions were made by entomologists in Canada (Swaine and Craighead, 1924) and the United States (Graham and Orr, 1940). These workers reached the conclusion that the outbreak developed and caused serious damage only where mature or overmature fir predominated in extensive areas, and made recommendations concerning the reduction of future losses through forest management. Foresters working during this early period also observed that high populations did not develop where the virgin mature forest had been broken into smaller units through the action of patchy fires or other factors (Webb, 1922). Studies of these relationships made after an outbreak must be very extensive, in order to be valid, and must include areas where the outbreak did not develop as well as the areas where it did. Outbreaks of the budworm attain great momentum in suitable forests and moth invasions may result in high mortality to balsam even in stands that are unfavourable for initial population development. Therefore "Post-mortem" studies, if restricted to the middle of an outbreak area, may easily fail to show what stand factors are important to population development. However, our life table studies during the development of the present outbreak show that these earlier observers were essentially correct. From the economic viewpoint, therefore, our present work does not present new and different suggestions for control; it merely substantiates the older ones and reveals the biological mechanisms through which forest conditions affect budworm numbers.

The possibility of reducing losses through forest management will be treated in more detail elsewhere. Unless the demand for pulpwood should fail, this type of control should eventually be achieved as the present reserves of overmature fir come under operation and management. The process can be hastened, however, if operators are induced to pay particular attention to the diversification of age classes so that future stands will mature in rather small blocks, and will be surrounded at maturity by younger stands or recent cutover. Where site conditions permit, the encouragement of other tree species and of mixedwood stands is also desirable. Until these conditions are brought about, repeated aerial spraying, as discussed by Webb (1957), appears to

offer the only hope of keeping trees alive for harvesting in accessible areas where man is now competing with the budworm for the existing stock of mature wood.

### ACKNOWLEDGMENTS

For very helpful criticism and suggestions concerning this paper we are greatly indebted to R. E. Balch, W. G. Wellington, and M. L. Prebble of the Forest Biology Division; and to Jost Franz of Darmstadt, who was kind enough to review the manuscript while visiting Green River.

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### DISCUSSION

J. FRANZ. The importance of small differences in behaviour for differences in susceptibility to climatic factors and, thereby, for variations in population dynamics might well be demonstrated by the following example. The spruce budworm is able to enter needles as well as closed buds. The European relative, *Choristoneura murinana*, is not able to mine and depends, therefore, much more on a perfect time coincidence of budding and emergence after hibernation than *C. fumiferana* does. Thus, detailed behaviour studies have to precede any quantitative approach to population problems.

R. F. MORRIS. I agree that the quantitative approach to population dynamics can be greatly aided by prior work on life history and behaviour, as well as by qualitative observations on the pattern of forest damage resulting from earlier outbreaks. In our life table studies on the spruce budworm we are fortunate in dealing with a species whose behaviour has already been carefully studied, and in having the benefit of working hypotheses based on extensive observations, like those of Dr. S. A. Graham, in an earlier outbreak.



C. M. BAETA NEVES. Je veux faire noter que si dans la forêt "climax" on considère le complex biologique animale et végétale complet, les études sur le dynamique des populations dans la forêt artificiale ne doivent considérer seulement les parasites mais tout les autres facteurs, surtout les microclimatiques, à qui on doit surtout la pullulation des insectes plus nuisibles à la forêt en Portugal où les parasites ont une importance secondaire.

G. C. VARLEY. If weather reduces a parasite population by chance when hosts are above average, the parasite may run up against the limit of egg supply — allowing the host to increase without restriction for some generations, before catching up and ending the outbreak.

G. H. PLUMB. Would Dr. Morris care to comment on some of the possible reasons why parasites are more effective on an intermediate spruce budworm population than on an epidemic population?

R. F. MORRIS. I shall mention two of the hypotheses that are currently being tested. First, work by L. G. Monteith and others suggests that some parasites show an olfactory response to the tree species on which their host insect feeds. It occurred to us that severe defoliation of balsam fir by the budworm might affect this response, so that parasites would not be attracted to severely defoliated trees. Olfactometer tests using the budworm parasite *Glypta fumiferanae* suggest that the parasite is, indeed, attracted to balsam fir in preference to foliage from trees that are not budworm hosts. So far, however, we have been unable to detect any difference in the parasite response to fresh balsam branches as compared to severely defoliated branches bearing many dead and dying needles. Secondly, under epidemic conditions budworm larvae suffer various degrees of starvation and it has already been mentioned that the mean fecundity of the resulting moths may be reduced to 75 eggs or less. Perhaps parasites that mature in starved host larvae suffer even greater reductions in fecundity or activity.

HENRY A. BESS. What about the efficiency in performance of spruce budworm parasites at low densities?

R. F. MORRIS. I don't believe that question can be answered until the present outbreak of the budworm is over and we have had an opportunity to study the post-outbreak, endemic level of population for several consecutive years.



# Life Tables for the Lodgepole Needle Miner *Recurvaria starki* Free. (Lepidoptera: Gelechiidae)<sup>1</sup>

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## ABSTRACT

A method for preparing life tables for the lodgepole needle miner, *Recurvaria starki* (Free.), is described and samples from two locations are presented. Conventional column headings are used with the omission of the life expectation column ( $e_x$ ) and the addition of the mortality factor column ( $d_xF$ ), suggested for spruce budworm life tables. The latter permits tabulation of the different mortality factors. The major mortality factor, winter climate, is discussed briefly in its role of reducing the outbreak populations. The two examples present different population histories, believed to be related to local climatic differences. Incomplete life tables are presented for the period 1948 to 1954; complete ones for the period 1954 to 1956. Life tables for the needle miner are compared with those for the spruce budworm on an equivalent scale. Future consecutive life tables for successive generations should provide fundamental information on the epidemiology of this species and on variations in a diverse climatic region.

## INTRODUCTION

The importance of life tables in epidemiological studies has become increasingly apparent since the review by Pearl and Miner (1935). Their attempts to formulate a general theory of mortality and their recognition of the necessity of following a statistically acceptable cohort of an organism throughout its life cycle to achieve this was perhaps the beginning of the intense interest which has since been generated. The extensive review by Deevey (1947) focussed ecologists' attention on the transition of demographic life tables to ecological life tables. The limiting factor to their use in ecology has been the development of suitable techniques for measuring natural populations. Prior to Deevey's review the use of life tables in ecology was recognized in few textbooks. Bodenheimer (1938) discussed the concept at some length for insects as well as mammals and birds. Leopold (1939) gave a comprehensive review of ecological life tables which he termed "life equations". Since Deevey's review at least three major ecological texts have devoted considerable space to discussions of life tables; these are: Allee, Emerson, Park, Park, and Schmidt (1949), Andrewartha and Birch (1954), and Odum (1953).

The use of life tables in forest epidemiology has lagged behind that for other organisms. Again, this is largely due to the lack of suitable sampling techniques. A form of life table for insect populations has been in use in Europe since at least the 1930's. Schwerdtfeger (1950), in his concise text "Grundriss der Forstpathologie", presents what is intrinsically a life table: that is, the graphic presentation of the "intra-cyclic change" for a generation of the Owl moth, *Panolis flammea* (Schiff.). These are linked for successive generations to compile "Gradation" or infestation curves. Varley, in 1947, published his intensive studies on the knapweed gall-fly, wherein he followed the reduction of populations as a result of mortality factors. His sampling periods were at very short intervals and intensive and he was able to describe the population reduction in great detail. Morris and Miller, in 1954, presented the first detailed example in North America of a life table for the spruce budworm. This excellent paper introduced a series which follows the development of techniques with the objective of compiling life tables for long-term epidemiological studies. This series, when completed, should stand as a model for future workers for a long time to come.

This paper synthesizes a similar series of investigations on an outbreak of the lodgepole needle miner, *Recurvaria starki* (Free). Studies relevant to the formation of life tables have been published, notably: sampling techniques for larval stages (Stark, 1952a, 1952b); the life history and the primary larval mortality factor (Stark, 1954;

<sup>1</sup>Contribution No. 370, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada. Ph.D. Thesis (part) Univ. British Columbia, February, 1958.

Henson *et al.*, 1954); and defoliation and damage studies (Stark and Cook, 1957). From these and other unpublished data it has been possible to formulate life tables which will enable us to follow systematically the population fluctuations of this insect. Partial life tables have been formed for generations from 1948 to 1954 but their accuracy and completeness leave much to be desired. The only excuse for their inclusion is that they demonstrate the importance of a single factor in larval population reduction.

**LIFE HISTORY OF THE INSECT:** Although further details on various stages in the life cycle will be discussed more fully, a general description of it (Fig. 1) will help in

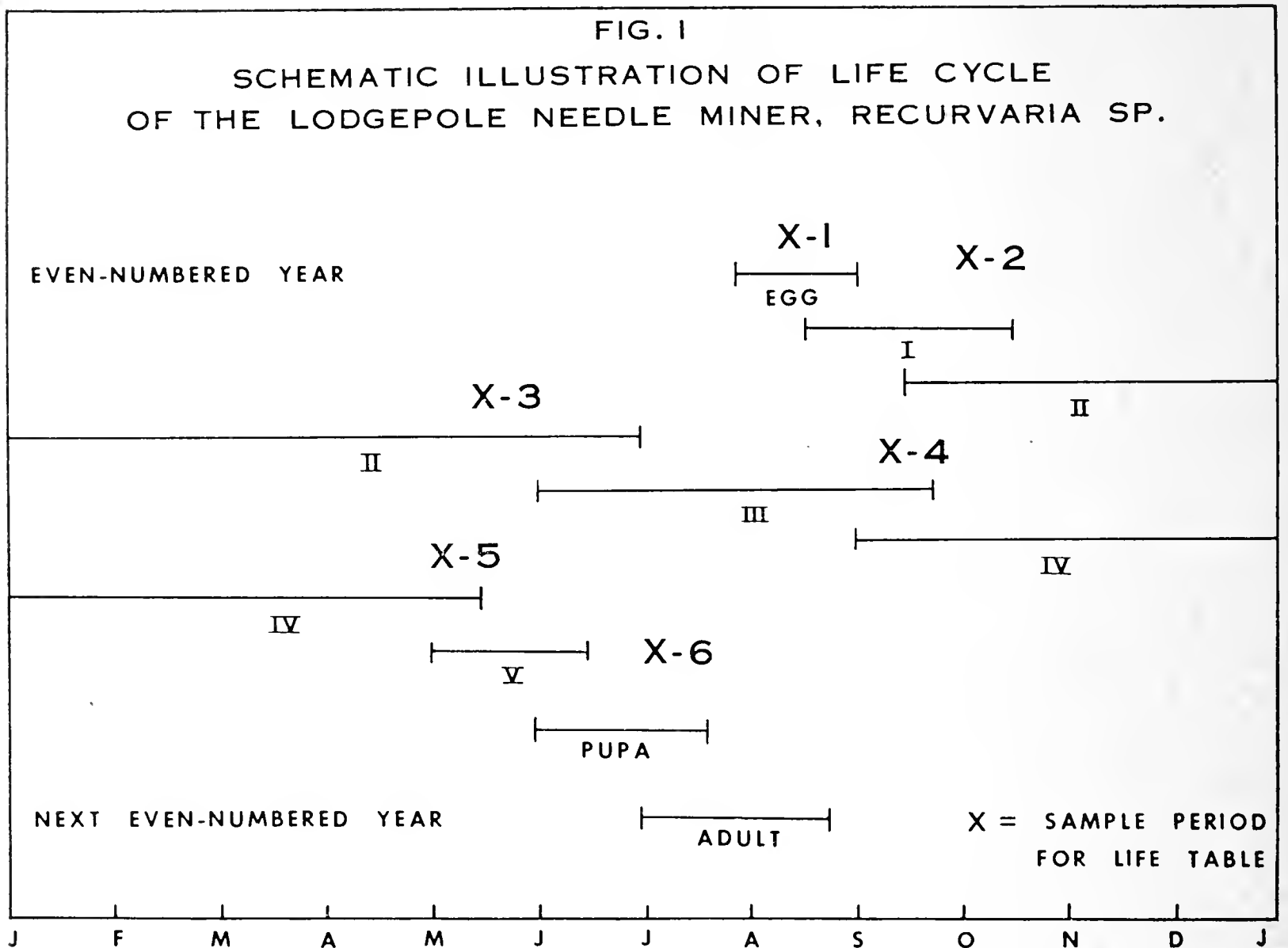


Fig. 1. Schematic illustration of life cycle of the lodgepole needle miner showing the sampling periods used in life table studies.

following the life tables presented. The needle miner in the Canadian Rocky Mountain Parks has a two-year life cycle. In the even years, 1952, 1954, 1956, the adults emerge in July, eggs are laid in late July and August, and hatch in August and September. Each larva immediately enters a needle in which it spends the first winter. The following spring, the miner commences to feed in late April or May and completes mining of the first needle. The transfer to the second needle takes place in mid-summer; climatic conditions affect the time and duration of the transfer period considerably. The larva overwinters in the second needle and the following spring, again an even year, transfers to a third needle. It completes mining this by early June, pupates and the moth emerges three to four weeks later.

**DESCRIPTION OF THE REGION:** The needle miner outbreak was concentrated in three National Parks: Banff, Yoho and Kootenay. The terrain is mountainous, the general character of the mountains being steeper and more rugged on the east side than on the west. The mountain ranges run in a north-north-west to south-south-east direction. The parks are similar in that there is in each a relatively narrow valley with steep, high sides formed by mountain ranges, mostly between elevations of 9,000 and 10,000 feet. Valley bottom varies in altitude from about 4,500 feet to almost 5,500 feet approaching the Continental Divide. The main valley in Banff Park has almost pure stands of lodgepole pine *Pinus contorta* (Dougl.) var. *latifolia* (Engelm.) with

isolated small patches of white and Engelmann spruce, Douglas fir, alpine fir, and trembling aspen. These stands vary in age from 35 to 200 years, although most are about 75 years old. All lodgepole pine stands in this region are a fire succession type. The stands in Yoho and Kootenay Parks are more variable, with fewer extensive stands of pure lodgepole pine.

**HISTORY OF THE OUTBREAK:** The outbreak was first noticed in 1942 (Hopping, 1946). The infestation was then restricted to a band between the 5,000 and 6,000 foot elevations. It was confined largely to Banff National Park and covered an area of approximately 50 square miles. By 1944 the area of the outbreak was approximately 300 square miles extending into all the adjacent parks. In the two succeeding moth flight years (1946, 1948), the infestation spread into practically all pine stands in Banff Park and adjacent areas in Yoho and Kootenay Parks. Recent studies on defoliation and increment of lodgepole pine (Stark and Cook, 1957) have led to the conclusion that the peak of the outbreak occurred between 1940 and 1944 and though there was a spread in succeeding years and local fluctuations, an over-all decline in numbers began with the 1944-46 generation. The outbreak has since declined until at the present time none exists. Although no tree killing occurred during the outbreak, defoliation reached levels greater than 75 percent and affected radial, terminal and lateral growth.

A short-lived outbreak was found in Jasper National Park in 1949 (Grant and LaRue) but it is thought to be autochthonous.

### LIFE TABLES FOR THE LODGEPOLE NEEDLE MINER

Little need be said concerning life tables in general. It is sufficient to note that the form used is that used in standard demographic tables, but with the inclusion of Morris and Miller's " $d_xF$ " column for mortality factors responsible for " $d_x$ ", and the elimination of the " $e_x$ " or life expectation column. Also, the manner of determining " $l_x$ " and " $d_x$ " is the same. That is, survivorship and natural mortality are measured by periodic sampling of the population. The resultant sampling error can be statistically evaluated. Complementary information is supplied by biological studies and insectary rearings.

The development of sampling techniques was not faced with as many difficulties as was that for the spruce budworm. Eggs of the needle miner are deposited in old, mined needles. The larva spends its whole existence within three mined needles except for the short time taken for transferring from one needle to another; it pupates within the last mine. Consequently the only truly mobile or dispersable stage of the needle miner is the moth stage.

Sampling intervals for the needle miner life tables are based more on "susceptible" stages rather than defined life stages. Experience has shown that the stages illustrated in Fig. 1 isolate the major mortality factors. The sampling periods, described in detail, are:

**$X_1$  — THE EGG STAGE:** The distribution of needle miner eggs in lodgepole pine trees is similar to that of the larvae (Stark, 1956). Oviposition is greatest in the upper crown, variability between trees arising from differences in crown length and stand density. The larva, upon hatching, usually mines a needle in the same tip if available, within a few hours of eclosion. It has been determined (Stark, 1952a) that upper crown samples give the maximum population estimate for a tree, mid-crown samples a reasonable average. For egg and larval sampling therefore, mid-crown samples are taken where time does not permit sampling all crown levels. Distribution of the eggs within oviposition sites (empty, mined needles) is relatively constant for any one area, and the five-year branch-tip sample basis developed for larvae is therefore adequate. The relationship of tree height to number of branch tips is known and the branch-tip samples are therefore convertible to a 'per tree' basis and from that to a per acre basis, if required. The time of sampling of this stage is naturally dependent upon completion of oviposition. Generally, this is about mid-August, but as the weather during this time affects both moth emergence and oviposition the progress must be checked. This is necessary as hatching usually commences within one to three weeks



after the completion of oviposition, leaving a limited period to make the sample. The sampling technique is necessarily slow and painstaking. Careful dissection of the needles is required for an accurate egg count. They are usually laid within a few millimetres of the moth emergence hole (Shepherd, 1950; Stark, 1954), but with disturbance frequently fall to lower levels in the needle. The eggs are large enough to be counted by the naked eye or with a low power hand lens. Sampling is continued until a mean number per five-year branch tip within set error limits is reached (standard error less than 10 per cent of the mean).

$X_2$  — FIRST LARVAL SAMPLE: This sample is taken in late September or early October and can be done without dissection of the needles. The new mines are thread-like and careful examination of the tips is necessary for accuracy. Entrance into the first needle is invariably into the distal quarter of the needle and almost invariably from the outside of the needle, that is, the curved surface. The needle epidermis over the fresh mines is a pale-green in contrast to the dark green of the unmined portions of the needle. Unsuccessful mines are also detectable without dissection. The larvae present may be first or second instar depending on the time of the sample; ecdysis usually occurs before winter hibernation. The advantage of sampling at this time is that it gives the established starting population and the loss of needle miner larvae between eclosion and establishment. New mines per branch tip are counted from as many tips as necessary to achieve the desired accuracy. This procedure is followed for all larval sampling.

$X_3$  — SECOND LARVAL SAMPLE: This is done after diapause is broken the following spring. Past studies by Henson *et al.*, 1954, have indicated that winter mortality is one of the major factors in population reduction. If the sample is left too late the larvae killed during the winter period dry and shrivel and are hard to find. A fairly accurate estimate can be made by counting the mines showing fresh feeding, and obtaining the mortality estimate by subtraction from the first larval sample ( $X_2$ ). However, if time permits, greater accuracy is obtained by actual counts of dead larvae. This permits a precise check of the previous autumn's sampling. A portion of the dead larvae are examined for incidence of disease.

$X_4$  — THIRD LARVAL SAMPLE: This sample determines the population entering the second winter's hibernation. Again, it is possible to do this without dissection of the needles by inspecting and counting the fresh mines. Third and fourth instar larvae are present in the autumn of the second year and are large enough to be seen in the mined needle. The population reduction over the summer can be determined by subtraction from the spring sample ( $X_3$ ). Mines in which the needle miner have been killed during the summer are characteristic, the pale green resulting from feeding drying to yellow as the summer progresses. As long as the larva lives the fresh feeding can always be distinguished. Experience has shown that this sample may be omitted without much loss in accuracy. Mortality during the summer of the 'larval year', even though a transfer from the first to second needle is effected, has always been extremely low.

$X_5$  — FOURTH LARVAL SAMPLE: This is an extremely important sample period as it shows the second winter's mortality and the larval parasite complex. Sampling must be done in the latter part of May and early June to ensure full development of parasites. Insectary rearings are a very necessary adjunct to check parasitism estimates and to obtain pertinent information on parasite biologies. Parasitism is not generally evident prior to this time except by larval sectioning or dissection. Again, a portion of the larvae found dead are examined for incidence of disease.

$X_6$  — PUPAL SAMPLING: After moth emergence, careful examination of pupal cases will yield information on pupal parasitism, mortality from other causes, the moth population and sex ratio. However, it is much simpler and more in keeping with the principle of life tables to obtain this information from mass insectary rearings and to check these results with limited field samples. It is possible at the time of the last larval sample to differentiate the status of each miner examined without undue disturbance. Once recorded for the purpose of that sample, they may be placed in the insectary and

TABLE I — Development of Life Tables for the Lodgepole Needle Miner.  
Mt. Eisenhower — Valley Bottom, 4800 feet.

1948-1950				
x — Age Interval	1 <sub>x</sub> —No. alive at beginning of x	d <sub>x</sub> F — Factors responsible for d <sub>x</sub>	d <sub>x</sub> — No. dying during x	100q <sub>x</sub> — d <sub>x</sub> as percentage of 1 <sub>x</sub>
Sept. 1948 — June 1949. I and II instar	3015	Climate — winter temperatures	932	30.91
June 4, 1949. Instars III and IV	2083	Climate — winter temperatures	1622	48.44
		Parasites	459	22.03
			2081	99.87
May 3, 1950. Instars IV and V	2			
Pupae — no sample				
Assumed emerged				
Moths SR 50:50	M 1	F 1		
GENERATION			3013	99.93
Expected eggs — ca 24				
Actual not measured				
Established larval population — 25; Population trend (larvae) — 0.8 percent				
1952-1954				
From eclosion to May 12, 1953. I and II instar	505	Climate—winter temperatures	26	5.2
May 12, 1953. II, III and IV instars	479	Climate — early winter temperature	21	4.3
Dec. 16, 1953. III and IV instars	458	Climate — January extreme minima	434	94.69
Feb. 5, 1954. III and IV instars	24 5	Climate — winter temperatures	19	79.17
June 2, 1954 — V and pupae				
Moths SR 50:50	M 2.5	F 2.5		
GENERATION			500	99.01
Expected eggs — 60				
Actual number eggs not measured				
Established larval population — 98; Population trend (larvae) — 19.40 percent				
1954-1956				
Eclosion to Dec. 13 I and II instar	98	Climate — fall and early winter temps.	83	84.23
Dec. 13. II instar	15	Climate — late winter temperature	7	46.67
Summer 1955	8	Climate — winter temperatures	8	100.00
June 26, 1956	0			
GENERATION			98	100.00
Expected eggs = 0				

TABLE II — Development of Life Tables for the Lodgepole Needle Miner.  
Mt. Eisenhower — 5400 foot elevation.

1948-1950				
x — Age Interval	1 <sub>x</sub> —No. alive at beginning of x	d <sub>x</sub> F — Factor responsible for d <sub>x</sub>	d <sub>x</sub> — No. dying during x	100q <sub>x</sub> — d <sub>x</sub> as percentage of 1 <sub>x</sub>
Eclosion to 1949		Climate — winter temperatures	927	23.23
I, II and III instars	3990			
June 1, 1949		Climate — winter temperatures	2199	71.80
III, IV and V instars	3063	Parasites	450	14.68
		Total	2649	86.48
Pupae	414			
Moths SR 50:50	M 207	F 207		
GENERATION			3576	89.62
Expected No. eggs — 4968				
Actual not measured				
Established larval population — 2500; Population trend (larvae) — 62.7 percent				
1950-1952				
Eclosion to summer, 1951. I, II and III instars	2500	Climate — winter temperatures	500	20.00
Summer, 1951 to spring 1952. III, IV and V	2000	Climate — winter temperatures	315	15.77
		Parasites	85	4.23
			400	20.00
Spring 1952	1600			
Pupae — no sample ass'd emerged				
Moths SR 50:50	M 800	F 800		
GENERATION			900	36.00
Expected No. eggs — 19,200				
Established larval population — 2709; Population trend (larvae) — 108.0 percent				
1952-1954				
Eclosion to summer, 1953. I, II and III instars	2709	Climate — winter temperatures	152	5.6
June 9, 1953. II, III and IV instars	2557	Climate — winter temperatures	219	8.55
Dec. 16, 1953. III and IV instars	2338	Mid-winter temps.	604	25.81
Feb. 2, 1954. III and IV instars	1734	Climate — late winter temperatures	248	14.30
		Parasites	236	13.60
		Total	484	27.90
May 25, 1954				
Pupae — not sampled — assumed emerged	1350			
Moths SR 50:50	M 675	F 675		
GENERATION			1359	50.17
Actual No. of eggs — 4,700				
Expected No. eggs — 16,200				
Established larval population—1114; Population trend—expected 598 percent, actual 173 percent				

TABLE III — Life Table for the 1954-56 Generation of the Lodgepole Needle Miner.  
Mount Eisenhower — 5,400 foot elevation.

x — Age Interval	$l_x$ —No. alive at beginning of x	$d_x F$ — Factor responsible for $d_x$	$d_x$ — No. dying during x	$100q_x$ — $d_x$ as percentage of $l_x$
$X_1$ — Eggs	4700	Needle drop larval dispersion Predators	3586	76.30
$X_2$ — Instars I and II	1114	Climate — late fall and early winter temperatures	409	36.68
Extra — Dec. 14, 1954	705	Climate — late winter temperatures	219	31.06
		Spring kill	70	9.93
			289	40.99
$X_3$ } Instars III and IV	416	Winter mortality	134	32.18
$X_4$ } July 1, 1955		parasitism	142	34.09
		spring kill	9	2.21
		Bird predation	1	0.30
		Unknown	7	1.68
			293	70.46
$X_5$ — Instars IV and V	123	Parasites	18	14.55
$X_6$ — Pupae	105	Unknown	26	24.76
		Parasites	< 1	0.45
			26	25.21
Emerged	79			
Moths SR 48:52	M 38	F 41		
GENERATION			4621	98.32

reared through to the adult stage. Field checks are necessary to avoid any artificial effect which may arise from insectary rearing.

These are the sampling periods deemed necessary to assess the course of the population of a single generation from the time of oviposition to moth emergence of the needle miner. To follow the course of successive generations it is necessary to link together the life tables of each generation through the reproductive stage. The comparison of starting populations after each moth flight will give the trend of the outbreak but does not yield any information on the critical reproductive stage.

The determination of fecundity of needle miner moths is difficult. Mating of moths and inducing them to lay eggs in captivity has met with limited success. In attempts made in 1956, the maximum number of eggs laid by a single female was 17. It has been necessary to dissect virgin and mated females and estimate, from the fully formed eggs in the ovary, the potential number of eggs. Dissection in past moth years has indicated from 16 to 30 eggs; results for 1956 are not yet available. For the purpose of calculating the number of eggs expected in the life tables presented, an average of 24 was used. That this number is probably high is indicated from the 1954 egg counts. Additional data from 1956 studies are expected to refine this estimate.

Life tables are presented for populations from the slopes of Mount Eisenhower in Banff National Park. The sample area is located 22 miles northwest of the town of Banff, on the east side of the Bow Valley. The examples are from two altitude levels: valley bottom (4,800 feet) and an elevation of 5,400 feet. Partial life tables based on actual samples are presented for three generations for the valley bottom (Table I) and four for the higher level (Tables II and III). Only the 1954-56 generation life tables follow the system described for their formulation.

EXAMPLE 1. MOUNT EISENHOWER — VALLEY BOTTOM: This requires little discussion. Life tables for the 1948-50 and the 1952-54 generations are incomplete but the sample periods are so timed as to show the major mortality factors. The life table for the 1954-56 generation shows that there was no measurable population after the winter of 1955-56.

The number of larvae present per 100 tips in the  $1_x$  column are based upon actual samples statistically evaluated and indicate estimated numbers within plus or minus ten percent of the mean. The established larval populations following the 1948-50 and 1952-54 generations agree fairly well with the expected number of eggs.

What is demonstrated clearly by these tables is the existence of three periods when mortality factors may drastically reduce the larval population. These are during the two overwintering periods and when parasitism becomes effective in the spring of the last year of the life cycle. In the winter of 1949-50, January extreme minima accounted for 78 percent of the population. In the winter of 1953-54, between December 16 and February 5, almost 95 percent of the population was wiped out. In the winter of 1955-56 the whole measurable population was killed.

The survivorship and death-rate curves for the 1952-54 generation are presented in Fig. 2 with those from the 5,400 foot elevation for comparison. The mortality

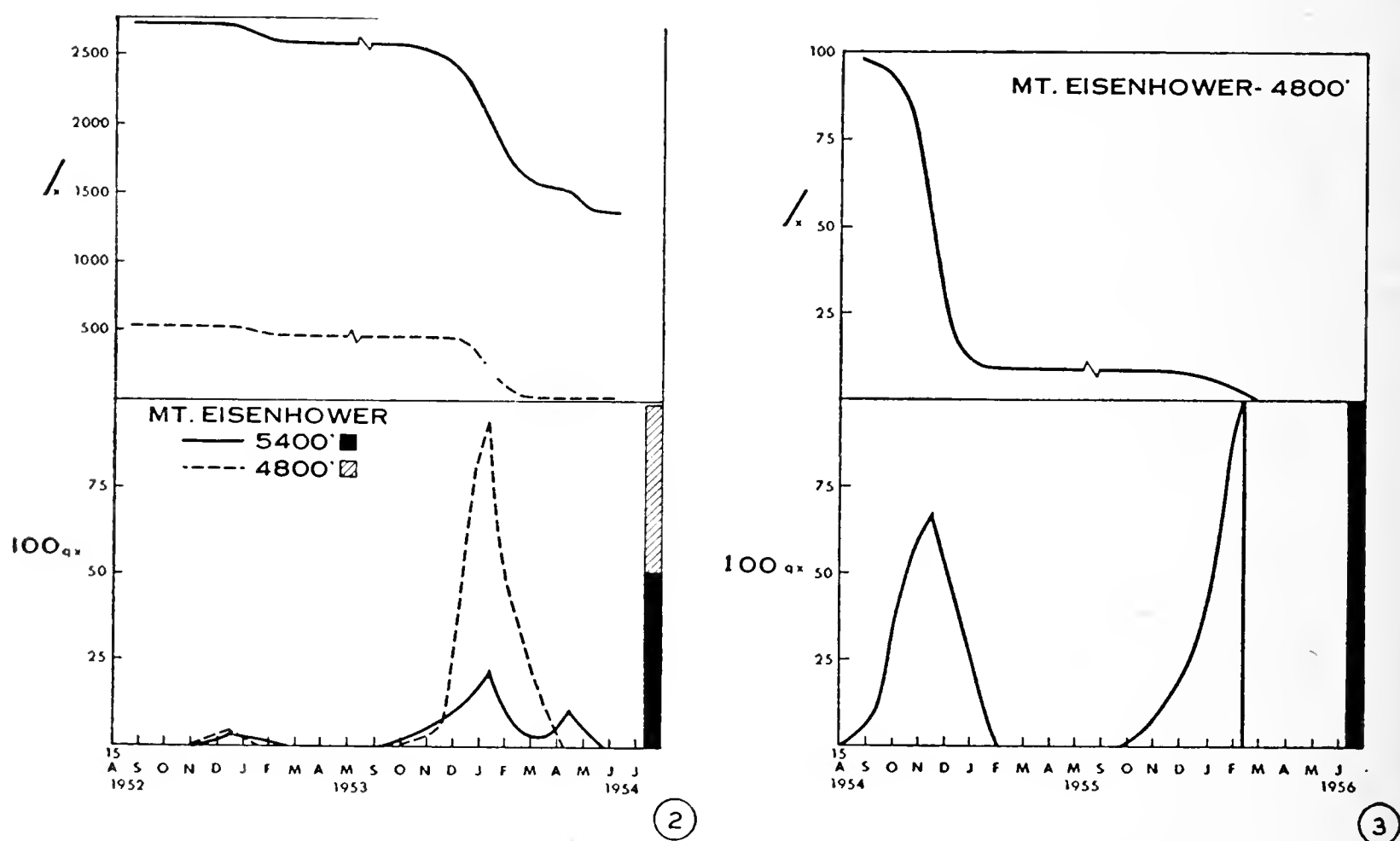


Fig. 2. Survivorship and death rate curves for the 1952-54 generation from both areas on Mount Eisenhower.

Fig. 3. Survivorship and death rate curves for the 1954-56 generation, Mount Eisenhower valley bottom.

periods described above appear as steps in the survivorship curve, that of the second winter and parasitism forming more or less a single long step, as parasitism becomes effective immediately after activity commences in the spring. The bar to the right in the death-rate curve represents the percentage mortality of the total generation.

Fig. 3 presents the survivorship and death-rate curves for the 1954-56 generation of needle miner at valley bottom.

EXAMPLE 2. MOUNT EISENHOWER — 5,400 FEET: This example is the more complete, as, following the severe winter of 1949-50 when it appeared that the high elevations offered "refuge" areas for the needle miner (Henson *et al.*, 1954), sampling was continued more intensively there than at the lower level. The life tables are presented in Tables II and III.



These also demonstrate the importance of the two winter periods and of parasitism in the final year of the life cycle. The discrepancy between the first egg count made in 1954, the expected egg population and the established larval population indicates a fourth period in the life cycle during which great losses may occur. It is possible that this discrepancy is entirely due to the failure of the moths to lay eggs but it is felt that it is more likely due to excessive needle drop. In the " $d_x F$ " column for the 1954-56 generation, larval dispersion and predators have been listed as well as needle drop. Examination of the litter in the sample areas has indicated that needle drop is high and is therefore a likely mortality agent but no method of measuring it has yet been evolved. Examination of egg shells after eclosion indicated little, if any, mortality from predation or other causes. There may, however, be predation without visual evidence. Larval dispersion is unlikely but cannot be entirely discounted. Analysis of 1956 egg sampling data may substantiate the needle drop hypothesis as the number of

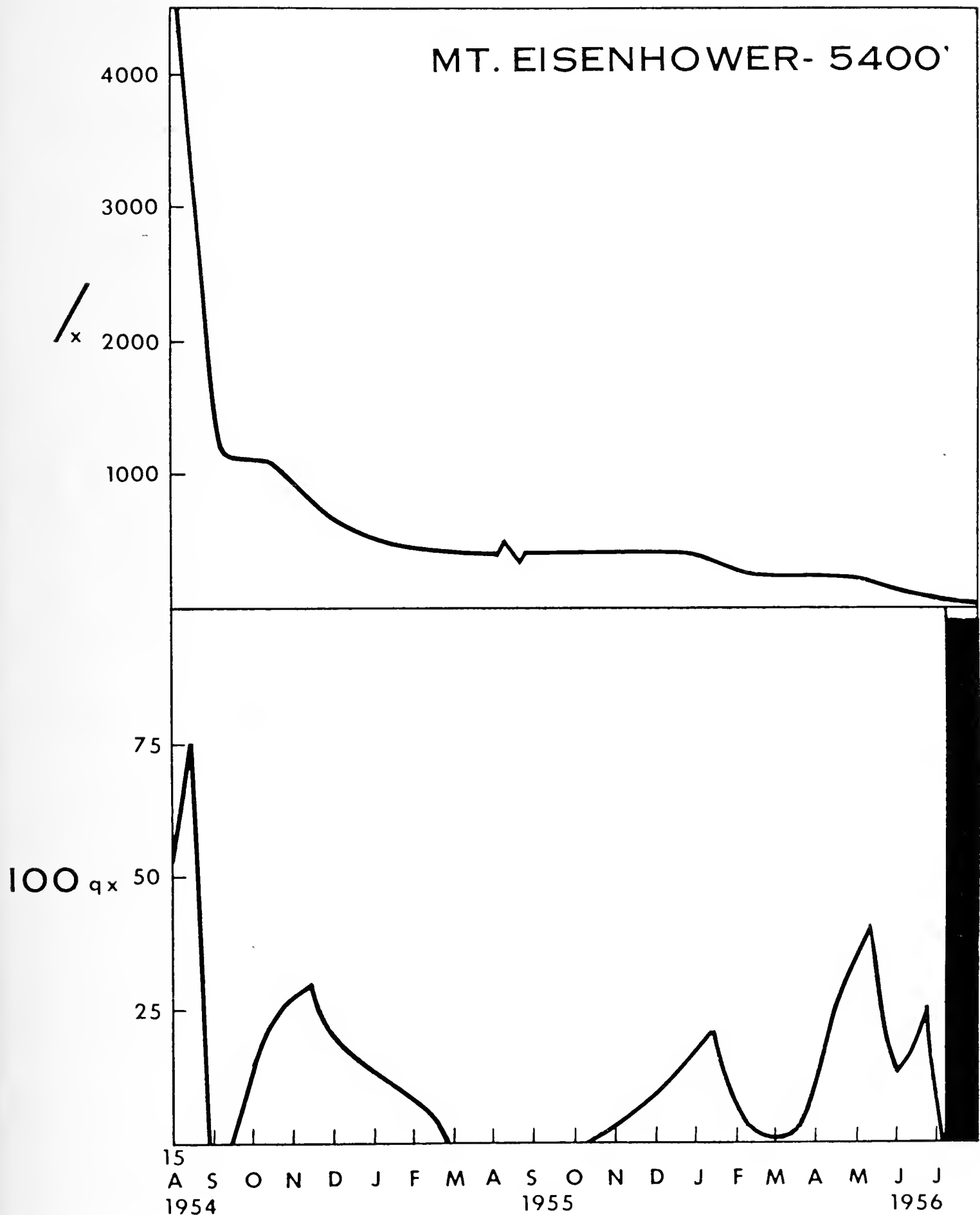


Fig. 4. Survivorship and death rate curves for the 1954-56 generation, Mount Eisenhower, 5,400 feet.

mined needles on branch tips is low and needle drop will be correspondingly low. The number of eggs found should, therefore, agree fairly well with the expected number of eggs (assuming our estimated number is accurate) and with the number of established larvae.

Survivorship and death-rate curves for the 1952-54 generations are presented with those for the same generation at valley bottom (Fig. 2). It is obvious that they differ only in degree and the curves emphasize the less rigorous conditions of the middle slopes.

The curves for the 1954-56 generation show the same general pattern, with the inclusion of the fourth mortality period at the beginning of the life cycle (Fig. 4). Tabulation of data to the emergence date shows that 98.3 percent of the total generation was killed; the first factor, needle drop or others, accounting for 76.3 percent, the first winter mortality 8.7 percent, the second winter 9.2 percent, parasites and other causes 3.6 percent, and pupal mortality 0.5 percent.

The mortality factor operating in the period between egg-laying and eclosion is undoubtedly of the greatest importance in the epidemiology of the insect and while still conjectural it is believed to be due to excessive needle drop caused by high winds. Winter temperatures are the major factor affecting the established population. The studies of Henson *et al.* (1954), and several samples since this work was published, have led to the conclusion that winter mortality is largely due to extreme winter minima which occur periodically. These occur when extended invasions of very cold polar continental air remain relatively static over the area for some time. Very briefly, the explanation for the difference in effect of these cold temperatures at the two elevations is that the cold air remaining in the trough-like valley becomes increasingly cold at valley bottom and for some distance up the slopes due to radiational cooling. The intensity of the cold and the distance to which it extends up the slope are dependent upon the length of time it "stagnates" there. It may be likened to the water level of a lake. Fig. 5 and 6 show schematically how the winter of 1949-50 affected the general distribution of the needle miner.

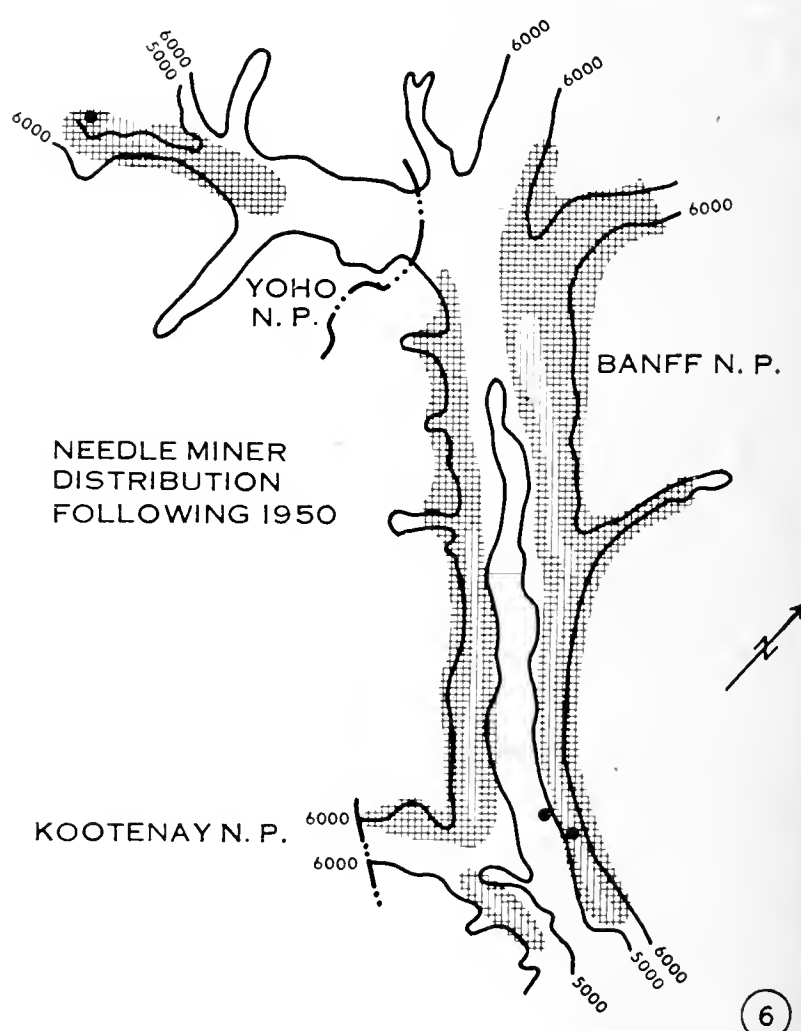
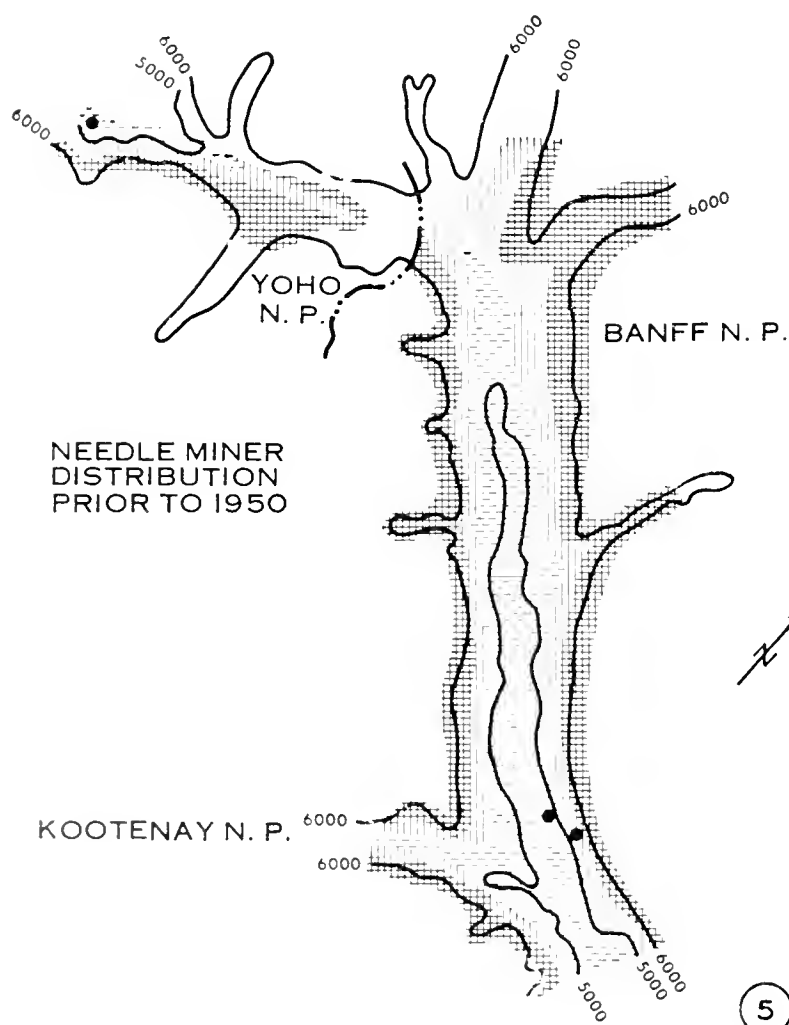


Fig. 5. Distribution of the lodgepole needle miner prior to the winter of 1949-50.

Fig. 6. Distribution of the lodgepole needle miner after the winter of 1949-50.

Although parasitism in the outbreak has been consistently low throughout the investigation period from 1948 to the present, indications are that it may be important

in the "refuge" areas, keeping the populations at a low level. At the higher elevations such as the one discussed, the numbers of the two most important parasites are apparently increasing.

Fig. 7 shows the comparison of survivorship curves for the spruce budworm (Morris and Miller, 1954) and the lodgepole needle miner. As the life histories differ

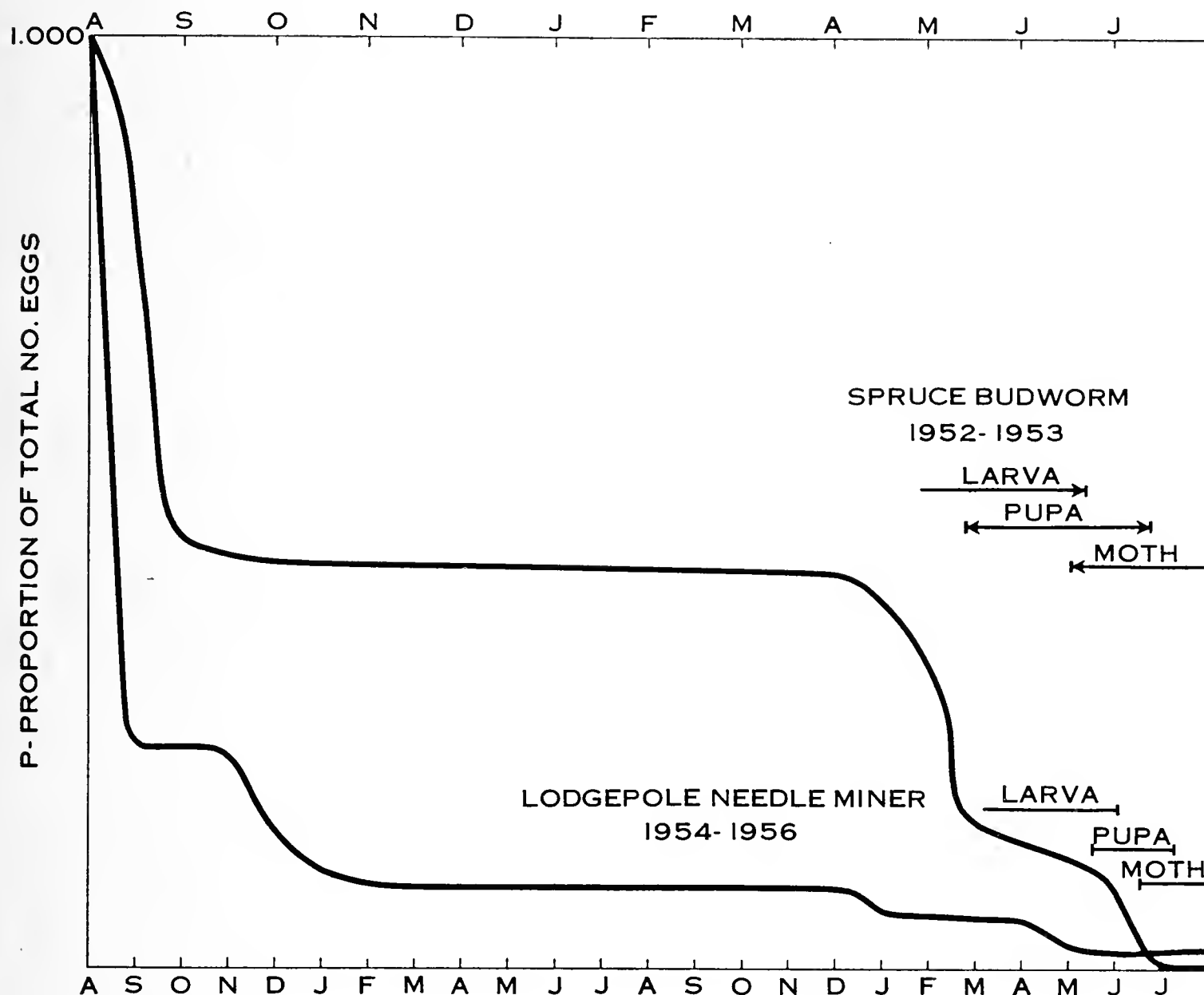


Fig. 7. Survivorship curves of the spruce budworm for the year 1953 compared with the lodgepole needle miner for the 1952-54 generation.

in length the time scales are made linearly equivalent. The population scales are made equivalent by converting  $1_x$  to a proportion of the starting population. Although the times of the mortality periods differ, the shape of the curves is remarkably similar, and, as Morris and Miller pointed out for the spruce budworm, the needle miner curves do not fit any of the "type" survivorship curves of Pearl (1940).

To summarize, the author has described the preparation of life tables for the lodgepole needle miner in our region and has compared life tables, and survivorship and death-rate curves from two areas, which demonstrate the fundamental importance of climate as a mortality factor. They also show clearly that there are four periods in the two-year cycle of this insect during which extensive mortality can occur. The actual mortality factors are well known in three of these periods and under study in the fourth. The fact that such "susceptible" periods exist throughout the life cycle of this insect and also the spruce budworm lessens the advisability of attempting to apply "formula" curves, such as those described by Pearl (1940), to survivorship studies in insects.

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# Studies on the Silvicultural Control of Conifer Aphids in Hokkaido, Japan

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## ABSTRACT

The todo-fir aphid, *Cinara todocola* Inouye, sucks the sap from the stems and branches of young todo-fir, and is the most destructive member of the conifer aphids attacking young forest trees in Hokkaido, Japan. The unthrifty condition of many todo-fir plantations in Hokkaido is attributed to infestations of this aphid (Fig. 1).

Of all the limiting factors in the aphid's environment, the physical, nutritional, and biotic factors are closely related to its rate of multiplication. The effects of temperature, light, moisture, wind, and rain on aphid fecundity and rate of development have been studied by many entomologists but information on these factors is still far from complete, especially on the relation between aphid populations and the amount of evaporation in the forest.

The writer has studied the biology and silvicultural control of this pest since 1934. This paper describes the infestation, life history, relation between aphid population and the amount of evaporation, and the technique of silvicultural control.

## SCIENTIFIC NAME, HOST PLANT, AND DISTRIBUTION

The todo-fir aphid, *Cinara todocola* Inouye<sup>1</sup>, occurs in Japan (Honshu and Hokkaido) and Saghalien. The recorded host trees are *Abies sachalinensis* Fr. Schm. and *A. firma* Sieb and Zucc.

## DAMAGE CAUSED BY APHID INFESTATIONS

**APPEARANCE OF AN INFESTATION:** The aphids attack young todo-fir trees and usually occur on the stem protected by various species of ants which conceal colonies of aphids within shelters constructed out of the material that they ordinarily use in making their own nests. The most important species is *Lasius niger* L. which builds shelters upward from the base of the stem sometimes covering the whole surface of the tree. The existence or size of the shelters apparently influences the lives of the aphids and their rate of increase.

The numbers of todo-fir aphids gradually increase from the middle of June and reach a peak at the beginning of August. Damage to young todo-fir trees continues until the end of September without any reduction of the population. The most active period of height growth of todo-fir trees is from June to July, when the aphids are feeding. A heavy aphid attack causes serious damage that shows mainly in the reduction of the growth of young trees and results generally in physiological deficiency. Young trees injured by aphids may therefore easily succumb to secondary insects, fungi, drought, cold, and other factors.

The aphid also exudes much honeydew which covers the needles, twigs, and branches. The honeydew is also a fertile medium for the growth of a black smut over the needles and branches, so that the trees appear as if they had been sprayed with some oily substance. Young trees are sometimes so weakened that they die after being infested for two or three years.

**INFLUENCE OF APHID ATTACK ON THE GROWTH OF TODO-FIR TREES:** As far as investigations on the populations in the Nopporo National Forest are concerned, the aphid checks the growth of young trees (Fig. 2).

Table I shows the relative rates of growth of infested and uninfested trees. None of the seedlings had ever been attacked by the aphids in the nursery. At the time of

<sup>1</sup>*Tuberolachnus todocolus* Inouye, *Insecta Matsumurana*, Vol. X, No. 4, pp. 131-134 (1936).

*Cinara todocolus* Inouye, *Hokkaido Ringyoshikenjo Jiho*, No. 33, pp. 18-19 (1941); *ibid*, No. 53, pp. 1-36 (1944).

*Cinara todocola* Inouye, *Special Report, Hokkaido Branch, Government Forest Experiment Station*, No. 5, pp. 208-238 (1956).





Figs. 1, 2. Young todo-fir trees attacked by *Cinara todocola* Inouye.

planting in the forest, the mean height of the seedlings in Group I (infested) was estimated to be  $43.63 \pm 0.92$  cm., and in Group II (uninfested)  $42.92 \pm 0.69$  cm. After four years, the mean height of these trees in Group I was estimated to be  $79.99 \pm 1.89$  cm. and in Group II  $98.48 \pm 1.25$  cm.

TABLE I—Comparison of the Growth in Centimetres between 18 Aphid-Infested and 13 Uninfested Trees.

Young todo- fir trees	Spring 1934	Average annual increment								Late 1937	
	Average	1934		1935		1936		1937		Average	
	H.	H.	D.	H.	D.	H.	D.	H.	D.	H.	D.
(I) Aphid- infested trees	43.63 ±0.92	9.94	1.39	3.38	1.02	8.64	0.08	14.40	0.53	79.99 ±1.89	2.66 ±1.05
(II) un- infested trees	42.92 ±0.69	8.18	1.71	5.96	1.49	17.16	1.19	24.89	0.72	98.48 ±1.25	3.20 ±0.73

H = Height                      D = Diameter at base

This difference is apparently the result of reduced growth increment in Group I caused mostly by severe aphid attacks since 1934.

The height growth of infested trees was evidently much less than that of uninfested trees although the former were slightly taller at planting time.

In late 1936, the mean diameter at the base of the young infested trees was  $2.66 \pm 1.05$  cm., and of the uninfested trees,  $3.20 \pm 0.73$  cm.

Measurements were recently made of the total height and annual height growth of infested and uninfested trees in a sample plot at the Hokkaido Prefectural Forest at Azuma, Yufutsu. Table II shows the difference of growth of infested and uninfested trees as indicated by average height and average annual height growth and the extent of the damage caused by aphid attacks.

TABLE II — Average Total Height and Average Annual Height Growth of Aphid-Infested Trees Compared with Uninfested Trees.

	Number of sample trees	Average total height (cm.)			Average annual height growth (cm.)	
		1952	1953	1954	1953	1954
Uninfested trees	58	89.8 ± 29.2	116.3 ± 36.1	133.3 ± 36.9	27.5 ± 7.1	15.6 ± 7.9
Aphid-infested trees	47	83.4 ± 24.2	101.2 ± 28.2	107.6 ± 31.0	18.2 ± 10.6	6.5 ± 6.1

LIFE-HISTORY

The life-history of the aphid in Nopporo National Forest has been reported in detail by the writer (1944). Temperature, precipitation, and aphid population records are shown in Fig. 3.

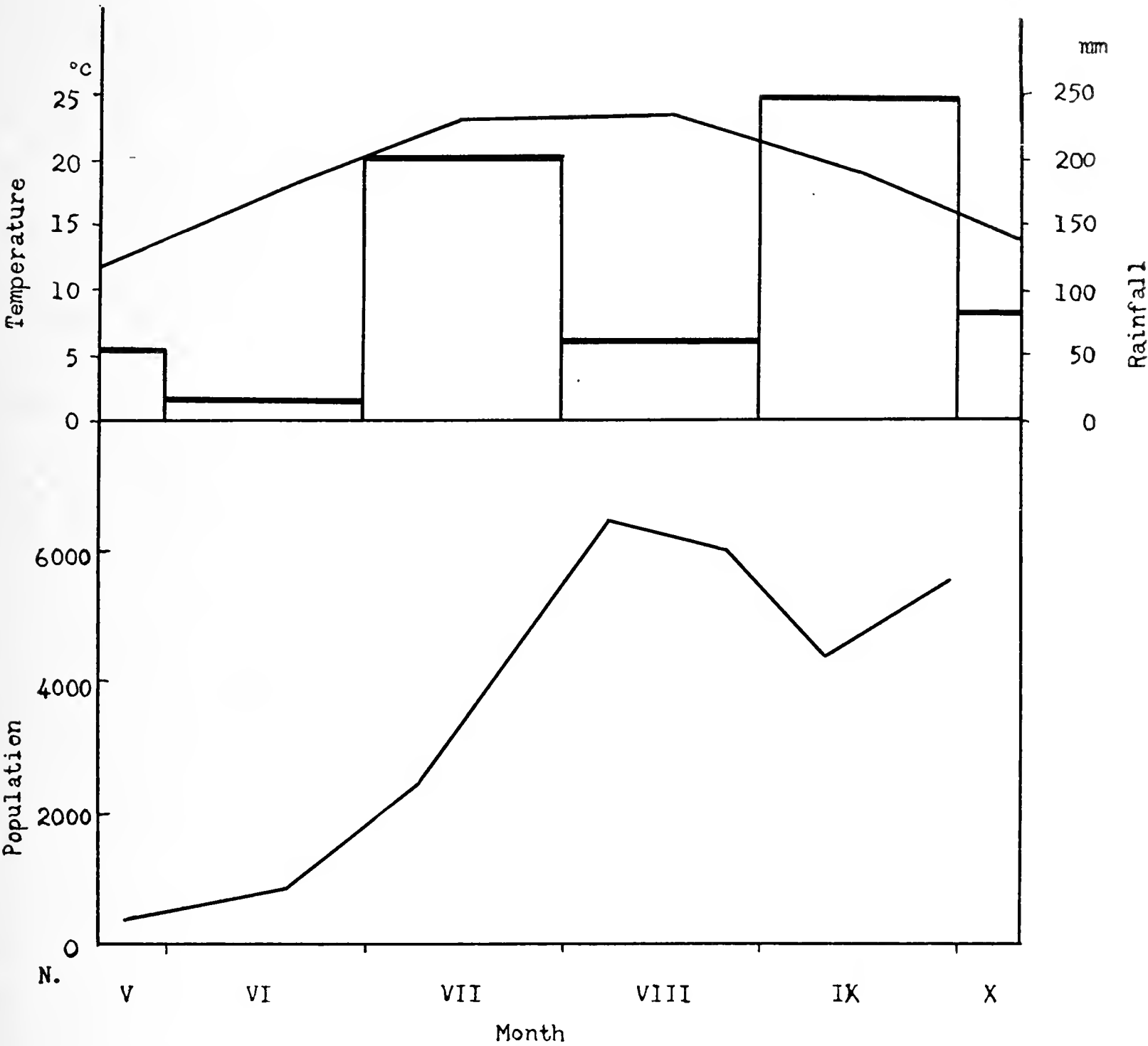


Fig. 3. Seasonal trend of populations of *Cinara todocola* Inouye with the climatograph at Nopporo based on populations from 100 trees.

The aphid hibernates on the needles of the host plant in the egg stage. The stem-mothers hatch within the period of about May 1 to 20 and feed on the branches and trunks of the host trees. They develop to apterous viviparous females 17-23 days after hatching and give birth to their young early in June. Most of the young develop into alate viviparous females (II generation), while others develop into apterous viviparous females in the first two weeks of July.

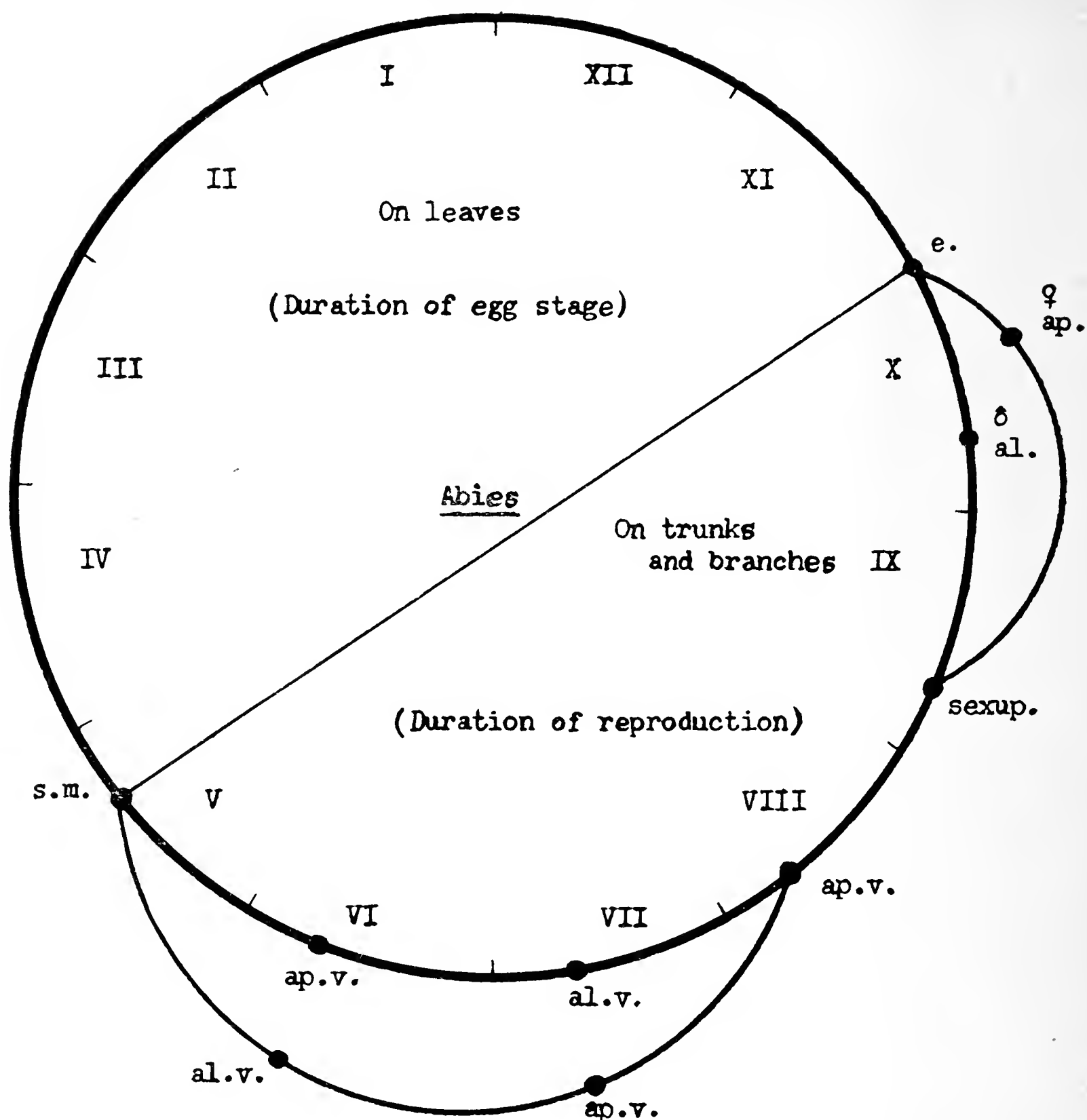


Fig. 4. Life history of *Cinara todocola* Inouye. s.m. — stem mother, ap.v. — apterous viviparous female, al.v. — alate viviparous female, sexup. — sexuparae, e. — egg.

Alate viviparous females (II generation) fly from tree to tree, and give birth to their young (apterous form) on the host plant. Apterous viviparous females (II generation) give birth to their young, of which the greater part develop into the alate form (III generation).

During summer the parthenogenetic generations follow each other in rapid succession. As shown in Fig. 4, however, alate males and apterous sexual females may be found in the middle of November. After mating, the females deposit their eggs on the needles of the host plant. The number of eggs within the sexual females ranges from 2 to 15. The adults normally perish before winter under forest conditions.

#### THE RELATION BETWEEN THE POPULATION OF THE APHIDS AND THE AMOUNT OF EVAPORATION IN THE FOREST

This aphid is injurious to young todo-fir in plantations, and there are sharp fluctuations in population correlated with the density of the over-story. It was observed that the amount of evaporation in dense stands was much less than that in open stands.

The factors which promote the amount of evaporation in the forest include high temperature, low humidity, intensity of light, and circulation of air. The crown canopy, therefore, regulates the amount of evaporation.

Measurements of evaporation in plantations were taken using Hirata's paper evaporimeter at the Nopporo National Forest. Fig. 5 shows how the aphid population is influenced by the amount of evaporation in the forest.

The Nopporo National Forest is a hill forest located in the southern part of the Ishikari plant; it consists largely of todo-fir, together with some white oak, sen, Japanese linden, maple, ash, Japanese elm, and some other trees.

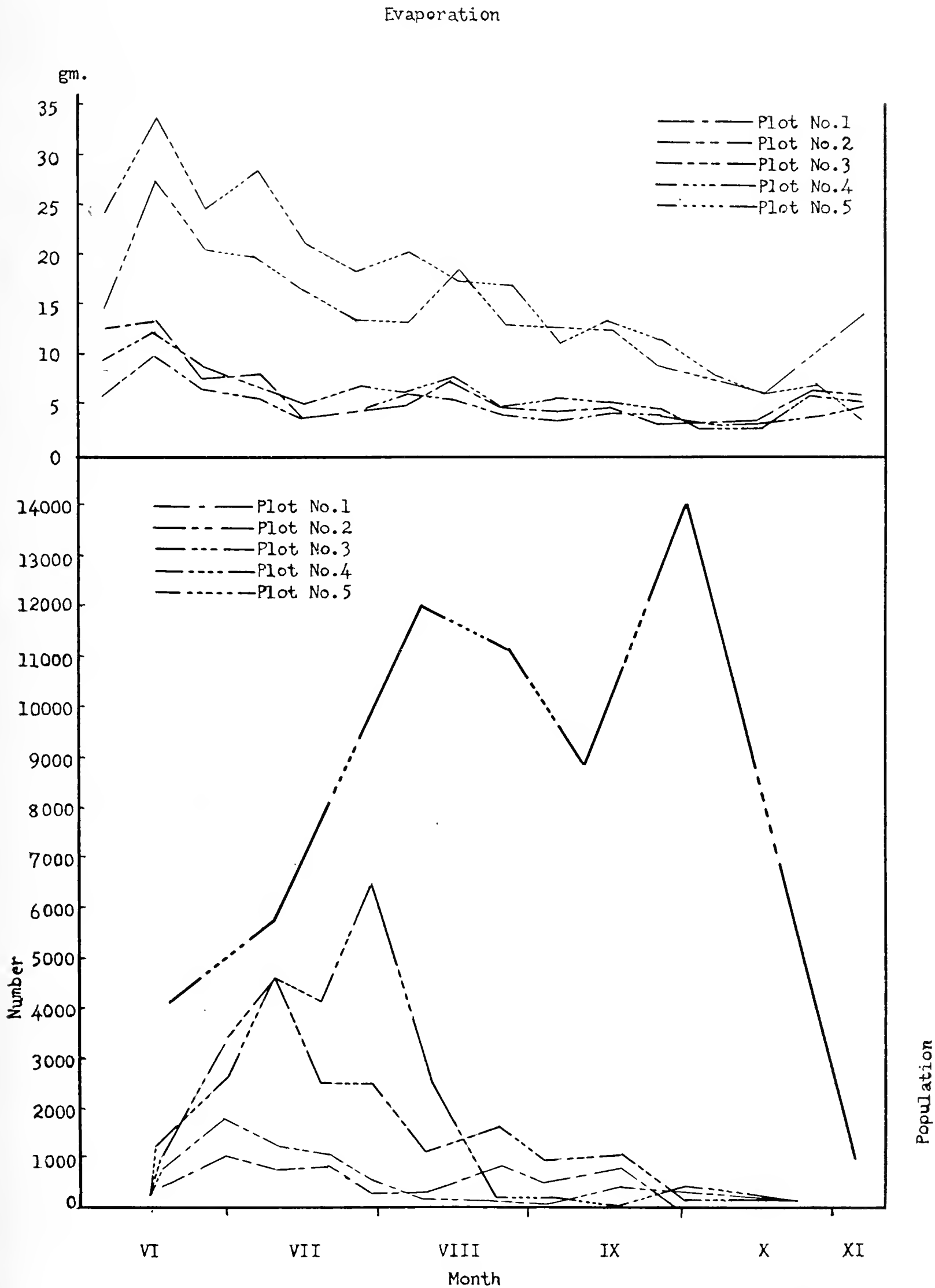


Fig. 5. Correlation between the aphid populations and amount of evaporation in Plots 1 to 5.

Experiment plots 1, 2, 3, and 4 consisted of 75-80% todo-fir trees which were 20 metres in height and 200 cubic metres in volume. Plots 1 and 2 were on uncut areas characterized by moderately dense crown canopy; Plots 3 and 4 were on areas cut on the gap selection system. The size of Plot 3 measured approximately 20 metres square, surrounded by trees of the same height. The size of Plot 4 measured approximately 50 by 20 metres, a little wider than Plot 3. Plot 5 was a young todo-fir plantation that was established in 1934 after clear-cutting, and contained some herbaceous plants and sasa bamboo.

In each experimental plot, 4-year-old seedlings were planted 20 per plot, leaving 2 metres distance between rows of seedlings.

Fixed adults of apterous viviparous females were reared on these planted seedlings in each experimental plot from the middle of June to the beginning of October. The average numbers of aphids per period of ten days in each month were recorded. Measurement of the amount of evaporation in each plot was made at 10 a.m. daily.

It was determined that the amount of evaporation decreased and that the aphid populations were also reduced in Plots 1 and 2 which had a moderately dense crown cover. The aphid population increased moderately, with a corresponding increase in the amount of evaporation in Plots 3 and 4 cut on the gap selection system. Aphid populations were greatly increased and the amount of evaporation was correspondingly great in open stands after clear-cutting as in Plot 5.

From the above data young todo-fir under a crown canopy were evidently less subject to attack by aphids than were those planted in open stands.

### SILVICULTURAL CONTROL

The natural development factors in the life of a forest include soil, nutrition, ground cover, micro-organisms in the soil, light, temperature, water, wind, and frost, all of which are involved in the development of a forest from youth to maturity.

As natural virgin forests are always covered by the crown canopy, there are distinct differences in physical conditions between dense and open stands. It is shown

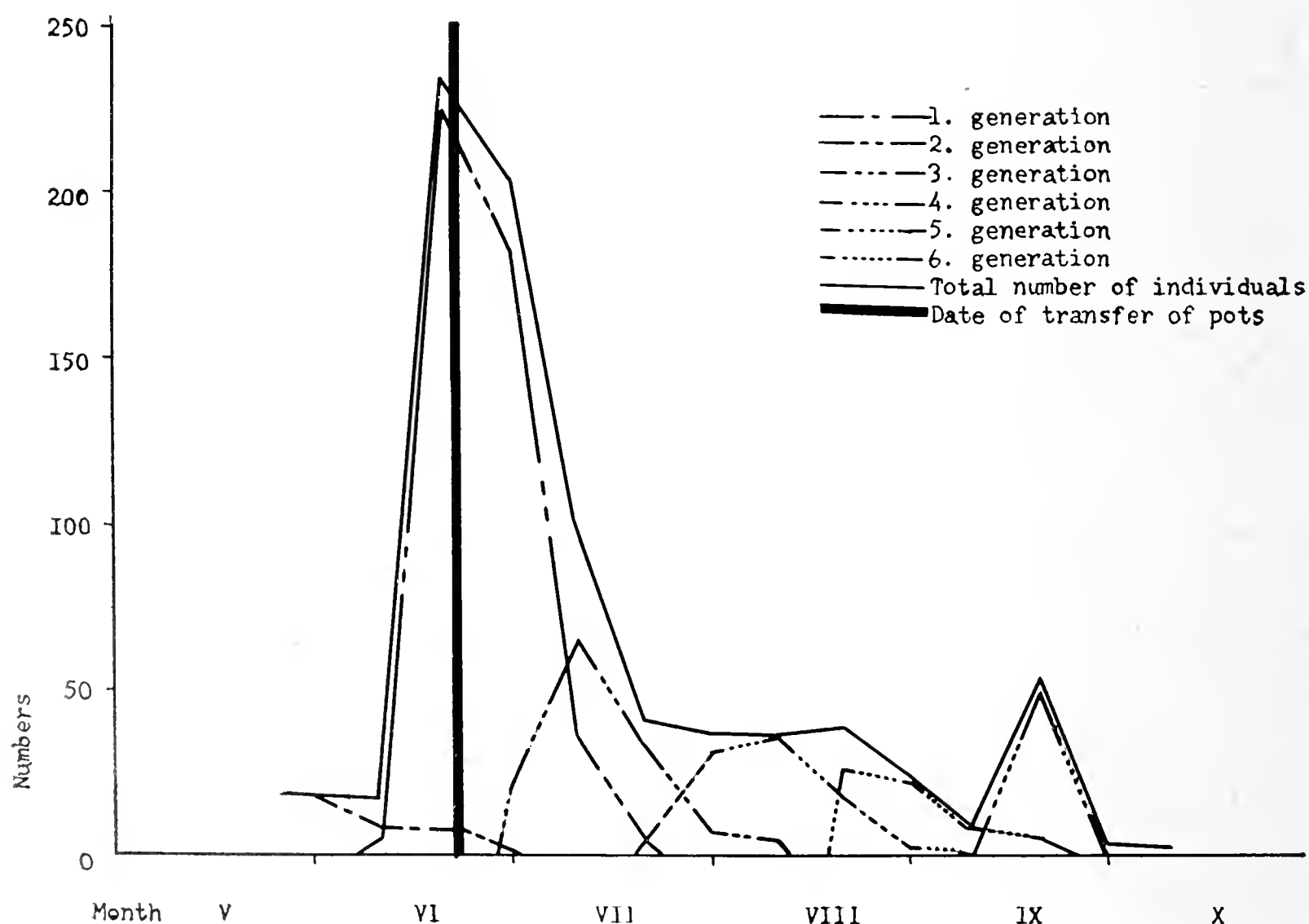


Fig. 6. Seasonal trend of aphid populations under dense crown cover at Nopporo National Forest. The peak of population is shown on June 22 in open stand just before transfer of potted trees under dense canopy.



in this paper that dense stands are much less susceptible to aphid injury than are open stands. Site conditions have, therefore, an important influence on the susceptibility of young todo-fir trees to aphid injury. Young todo-fir growing on a good site are adapted for thrifty growth and are relatively resistant to aphid injury.

The following investigations were carried out in order to obtain definite data on the influence of forest density.

Twenty potted 4-year-old todo-fir seedlings were placed in a clear-cut open stand. From the middle of May to the end of June the young trees became naturally infested by the aphid and populations greatly increased. The pots were then transferred to Plot 1 under dense crown cover. Fig. 6 shows the fluctuation in the aphid population.

At the beginning of the experiment the number of aphids present exceeded 200 individuals on June 22 just before the pots were transferred to Plot I; the number of aphids then decreased to less than 50 individuals under the dense canopy.

As shown in Fig. 5, the number of aphids on young todo-fir trees in the open stand was expected to increase from the end of June to September. It was proved, however, that the number of aphids greatly decreased under the dense canopy as shown in Fig. 6.

The amount of evaporation was also measured in open and dense stands by use of Hirata's evaporimeter; the results are shown in Fig. 7.

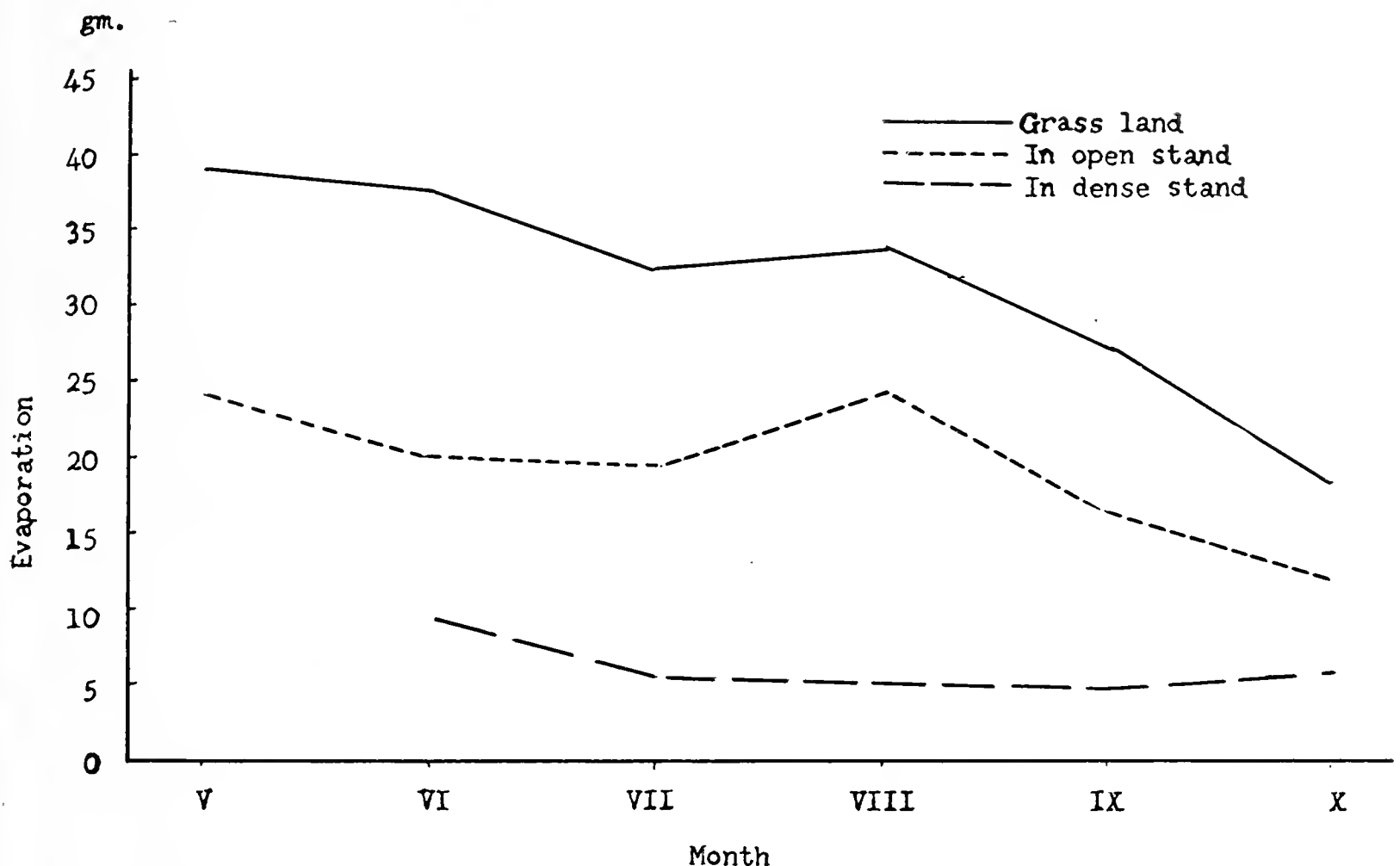


Fig. 7. Amount of evaporation recorded by Hirata's paper evaporimeter at Nopporo.

Forest density influences the physical conditions found in the forest by modifying such factors as temperature, light, moisture, wind, and rain.

The amount of evaporation as measured by Hirata's paper evaporimeter in the todo-fir forest has an important role as an indicator of aphid injury. In dense forest where the amount of evaporation decreased to an average of 5 gm. or less per day, the aphid population may be greatly reduced. Clear cutting is therefore not recommended for the control of aphid infestations on young todo-fir trees.

### CONCLUSION

From the point of view of aphid control, it is advisable to plant todo-fir seedlings in the natural forest before cutting. If a selection cutting or gap cutting system is applied after the seedlings are established on the forest floor, these operations exert

less influence upon environment in comparison with the clear-cutting system, and will be effective as an indirect method of control.

Since the crown cover is effective in the control of the aphid, it would be advisable to preserve the remaining trees in the plantation until there is no further risk of injury.

In a locality where the trees have been seriously damaged by aphids, it would be advisable to apply the gap-cutting system opening to an area whose length and width would be nearly equal to the height of the surrounding trees. The clear-cutting system should be avoided if possible. If todo-fir trees are to be planted in clear-cut or recently burned areas where there is risk of an aphid infestation, mixed stands would be less susceptible to attack than pure todo-fir stands.

Another promising method of control is to plant todo-fir trees in a mixed plantation of tolerant broad-leaved trees that will provide the necessary crown cover to discourage aphid attack.

# Progress in Bark-Beetle Control through Silviculture in the United States

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## ABSTRACT

*Insects are the greatest cause of timber mortality in the United States, outranking fire by a ratio of 7 to 1. Of these, bark beetles are the most important single group of forest insects. They killed 4½ billion board-feet of saw-timber in 1952.*

*Direct methods of bark-beetle control through bark burning and penetrating toxic sprays have been used for many years, but for some beetles these methods have not given lasting forest protection. Since these beetles are indigenous to the forests they infest, they have important ecological roles in regulating forest density and age. Through a study of the natural role of bark beetles in forest ecology, it has been possible to work out silvicultural treatments which will prevent forest damage caused by some species. Some of the measures which can be taken are: improving vigor of tree growth, reducing the average forest stand age, controlling forest fires, and disposing of slash and windfalls.*

*Control of the western pine beetle through sanitation-salvage cutting of high-risk trees has been worked out in detail and has proven highly successful. Clues to cultural control of some other bark beetles are available, but have not been developed to the point of practical application. Outbreaks of some bark beetles follow windstorms, fires, and droughts and hence cannot be entirely avoided.*

*Silvicultural control of bark beetles gives much promise of further success but has limitations which prevent it from becoming a cure-all.*

## IMPORTANCE OF THE BARK BEETLE PROBLEM

Control of bark beetles destructive to timber resources has been a major problem facing timber owners, foresters, and forest entomologists in North America since the turn of the century. A recent review of the timber resources of the United States, compiled by the Forest Service, U. S. Department of Agriculture, (1955), shows that insects were the greatest cause of timber mortality in 1952. As a killer of timber, insects outranked fire by a ratio of 7 to 1. Bark beetles were the most important single group of forest insects, accounting for 90 per cent of the insect-caused mortality of saw-timber, or a total of 4½ billion board feet. Most of this damage was in the western half of the United States. The destruction of timber by these beetles since 1910 easily exceeds 60 billion board feet. This stupendous loss of stored timber capital has spurred the efforts of foresters and entomologists to find an answer.

Solution of the bark beetle problem has been approached in two ways, (1) by direct control, through killing the offending beetles, and (2) by indirect control through application of forest management and silvicultural practices.

## FIRST THEORIES ON CONTROL

The first theories on control were simple enough. Since bark beetles were evidently causing the trouble, all that needed to be done was to kill the largest number of beetles at the least possible cost. Fire was a useful tool for this purpose. So, much of the early control work consisted of finding infested trees during the fall, winter, and spring months, felling such trees, and burning the bark—sometimes merely peeling the bark and exposing the immature beetles to the elements. As timber increased in value and bark beetle epidemics occurred, control projects grew in size and importance until as much as \$3,000,000 was spent on one project in a period of three years.

Through research many newer methods of bark beetle suppression were tried. Most failed; a few were successful. The best of these were oil-fumigant formulations. These direct methods reduced timber losses when applied against certain of the more aggressive bark beetles but made little impression on the course of epidemics of other

<sup>1</sup>Formerly with the Forest Insect Investigations Division of the U. S. Department of Agriculture, now retired.

species. The trouble was that while direct control reduced beetle populations, it did not change the susceptibility or resistance of the host trees. For instance, on areas of ponderosa pine where intensive direct control was applied, timber went right on dying after the beetle population had been reduced to a minimum, thus showing that the beetles were secondary to tree condition.

### ROLE OF BARK BEETLES IN FOREST ECOLOGY

During the early 1920's, forest entomologists and foresters dealing with bark-beetle problems came to realize that, since these bark beetles were indigenous to the forests they were infesting, they undoubtedly had a role to play in forest ecology and might be controlled through the application of silvicultural principles.

Munns and Colville (1928) at the 4th International Congress of Entomology at Ithaca, New York, were the first in this country to show how forest insects might be controlled through silvicultural practice. They stated: "That silviculture . . . may be used with beneficial effect in the control of insects, has not been greatly considered here in America by foresters. That it can be so used, however, should be kept in mind by all foresters and entomologists, for it is through silviculture that we can, first of all, arrest the development of epidemics and second assist in actual control work . . . The recognition that forest entomology was but one phase of silviculture — albeit a very important one — is only about 5 years old." Their paper was excellent in showing some of the silvicultural tools that might be used in preventing insect attack, such as regulating forest composition, density, and growth rate; and the proper handling of slash and fire. It should be of interest to reread Munn's and Colville's paper in order to measure the progress that has been made between the setting forth of principles at the 4th International Congress of Entomology and the developments in practice as we find them today at the time of the 10th Congress. The principles are still sound, but much development in practice still remains to be accomplished.

Killing certain trees is Nature's way of regulating forest density, eliminating understory trees that are competing with stronger trees for light, nutrients, and moisture, and disposing of the old overmature trees to make room for new generations of young trees. Thus the idea developed that one possible way to control bark beetle depredations was to find out what forest conditions favored their outbreaks and then to develop cultural practices to eliminate the predisposing causes.

Outbreaks of bark beetles require two principal sets of conditions, namely, (1) biological factors favoring development of a large population of beetles, and (2) a quantity of susceptible host material. Lacking either of these two ingredients an outbreak will fail to develop. Direct control considers only the reduction of beetle populations. Sometimes this is enough. Other times, it is more effective to reduce the quantity of susceptible host material. Control of bark beetle outbreaks must work toward the two goals of preventing large population build-ups and reducing susceptible host material.

### FACTORS INFLUENCING THE PRODUCTION OF BARK BEETLE POPULATIONS

Five factors are important in favoring an increase in bark beetle populations:

(1) **AVAILABILITY OF BARK BEETLES:** Of course, an outbreak cannot occur unless bark beetles are present. But in our native forests, they are always present. Because of their biotic potential, they can increase rapidly if environment and food are favorable. Even when the beetles are nearly wiped out by cold weather or other factors, their recuperative powers are tremendous, and they can quickly restore their normal populations. For this reason direct control can never be more than a temporary palliative, and extermination is unpractical, if not impossible.

(2) **VIGOR OF THE BARK BEETLE SPECIES AND STRAINS:** Some bark beetle species are characteristically more aggressive than others, and some strains may be more potent. The possibility of a change in insect vigor has not been fully explored.

(3) **NATURAL CONTROL FACTORS:** Absence of predators, parasites, and other natural control agents favor beetle build-up. While these factors are recognized as important, we still do not know how to evaluate their effectiveness.

(4) **WEATHER AND ENVIRONMENTAL CONDITIONS:** Warm, dry years favor production of most bark beetles; cold, wet years discourage them. Optimum temperatures for most species range between 50°F and 80°F. Certain moisture and environmental conditions are also required to give bark beetles their optimum breeding conditions. Weather works not only directly on the beetles but indirectly through the host.

(5) **ABUNDANCE OF FOOD SUPPLY:** An abundant food supply is obviously an essential requirement for developing a bark beetle outbreak. Here we are dealing with the quantity of susceptible host material.

## FACTORS INFLUENCING THE SUSCEPTIBILITY OF THE HOST TREES

Among stand conditions that make for greater bark beetle activity, three stand out:

(1) **TREES FRESHLY KILLED BY CAUSES OTHER THAN BARK BEETLES:** The phloem of freshly killed trees, such as in windfalls, snowbreak, lightning-struck trees, fire-killed trees, cull logs, and slash is favored as a breeding medium by almost all bark beetles. They breed freely in this kind of host material, selecting their normal host trees and the portion of trees they prefer to attack. If this killed material is abundant, beetle populations may develop and cause serious outbreaks in living timber.

(2) **TREES WEAKENED BY DROUGHT, DISEASE, OR OTHER INSECT SPECIES:** Drought, defoliating insects, fire, and some tree diseases, such as root diseases, needle cast fungi and mistletoe, weaken trees so that many trees or whole stands become susceptible to bark beetle attack.

(3) **SILVICAL CONDITIONS:** (a) Host tree resistance and susceptibility.

The age of trees has an important relation to their susceptibility. Many bark beetles favor trees of older ages, while some favor young trees. For each bark beetle species there seems to be an age at which the host trees become particularly susceptible to beetle attack.

In general, trees of slow growth and poor vigor are more susceptible to beetle attack than their more vigorous neighbors. In this category of low-vigor trees can be placed those affected by disease and mistletoe, or those that are suffering from injury, drought, or stand competition. Hetrick (1949) noted that "injuries to the roots of pine trees are of greatest importance in making trees attractive to bark beetles." Tree vigor is of decreasing importance as epidemics increase in intensity. During the height of bark beetle epidemics very few trees are immune to attack. Some beetles, such as the mountain pine beetle, the Black Hills beetle, the Engelmann Spruce beetle, and species of *Ips*, are conspicuous only when in epidemic numbers. At these times, large groups of trees are attacked apparently without regard to individual tree vigor, and yet during such epidemics a few of the strongest, most vigorous trees are able to survive.

Closely allied with tree vigor is the matter of tree health. Trees of apparently strong vigor may be currently sick from one cause or another, while trees of poor vigor and slow growth rate, such as those growing on rocky ledges, may be in good health. As in other living organisms a sick individual is much less resistant than a normal one, and a sick tree is definitely susceptible to bark beetle attack.

(b) Stand resistance and susceptibility.

Occasionally, large segments of the forest stand, rather than the individual tree, can be considered the unit of susceptibility. The environmental conditions under which the timber is growing have an important bearing on stand susceptibility to bark beetles. Low site due to insufficient plant foods or moisture contributes to poor stand vigor and often leads to high beetle losses.

Oftentimes, bark beetles play a role in determining ecological forest succession, so that age of forests is an important consideration in determining susceptibility. Bark



beetles commonly remove temporary forest types and make way for the more permanent or climax type. Bark beetles are one of the natural agents which gradually deplete climax types in the process of forest succession. Thus for many forest stands there seems to be an "entomological rotation" age beyond which heavy timber losses may be expected as a result of bark beetle attack.

When stands become too dense, tree competition increases and stagnation sets in. Bark beetles are often nature's tool for relieving this pressure. If stands are periodically thinned much of this type of damage can be avoided.

Pure stands of a single species are often more susceptible to bark beetle attack than mixed stands. This same principle applies to the activities of many defoliators.

## CULTURAL CONTROL THROUGH APPLIED SILVICULTURE

### PRINCIPLES

It can be postulated that, if timber stands could be kept in a young, fast-growing, vigorous condition through cuttings or a short rotation, and were not subjected to fires, lightning, windstorms, nearby slashings, drought or stand stagnation, they would not be subject to bark beetle attack. Unfortunately this ideal condition can rarely, if ever, be realized. In spite of the highest degree of intensive forestry, the accidents of drought, lightning, and windfalls cannot be avoided, nor can fires always be controlled. Of course, prompt action following such natural catastrophes will do much to avoid breeding a beetle epidemic.

The best forest practices from the standpoint of reducing the bark beetle menace will be those that reduce or prevent forest fires, and promptly dispose of, or treat slashings, windfalls, lightning-struck trees, or those injured by forest fires or drought.

In addition, cultural practices for the purpose of bark beetle control will include measures to improve tree growth, to regulate density, to avoid stand stagnation, and to reduce the stand age, so that no part of the stand will be in excess of the entomological rotation age.

If, as we assume, these native beetles have been practising a primitive form of silviculture, as they must have been doing in their role as nature's thinning and harvesting agent, then our best clue is to find out how to make our forms of silviculture conform to nature's methods (Keen 1950).

### APPLICATION TO SPECIFIC PROBLEMS

The western pine beetle *Dendroctonus brevicomis* (Lec.) was the first bark beetle in the United States to receive attention from the silvicultural standpoint. Outbreaks of this beetle in the interior ponderosa pine type of northeastern California, eastern Oregon, Washington, British Columbia, and Idaho are characterized by sustained losses in trees of poor thrift. Outbreaks are favored by drought periods, stand stagnation, advanced age, or any condition which results in poor tree vigor, lowered growth rate, or poor health. Once an epidemic is underway, trees of good thrift may be taken.

After large-scale direct-control efforts in the early 1920's failed to do more than temporarily reduce damage to ponderosa pine forests of eastern Oregon and northeastern California, Dr. F. C. Craighead and E. N. Munns in 1923 suggested that probably the beetles were secondary to tree condition. They suggested that possibly more progress might be made through working with the host trees rather than trying to suppress beetle populations directly.

Studies were started in 1924 on tree resistance and susceptibility to beetle attack and it was soon found that this beetle selected the less vigorous, slow-growing trees in the early stages of epidemics (Craighead 1925b; Person 1928). Only after it had built up its populations to epidemic proportions, did the beetle kill the more vigorous fast-growing trees.

Comparison of a large sample of trees killed by this beetle with living trees showed that there was a high degree of selection of the less vigorous trees as indicated by crown position, size, and vigor. There was also a slight increase in susceptibility with advancing age (Keen 1936).

Setting up a tree classification of four age groups and four degrees of crown vigor in each age, the writer determined the actuarial risk of 16 tree classes and found that trees of the poor vigor classes were definitely the most susceptible (Keen 1943). The implications of this tree classification were further refined by Salman and Bongberg (1942) in adding the symptoms of current poor health.

Using these classifications as tree-marking guides, selective cuttings were made of virgin ponderosa pine stands in northeastern California and eastern Oregon (Orr 1942). Light cuts of as little as 15 to 25 per cent of the stand were possible when taking out only trees of highest risk. These cuts proved effective in reducing western pine beetle infestations by as much as 90 per cent in the first year and the results were at least 70 per cent effective for periods up to 15 years. Removal of high risk trees only has been termed "sanitation-salvage" cutting. It has proved effective in the interior ponderosa pine type east of the Sierra-Cascade divide, in California, Oregon, Washington and Idaho.

It has not been possible to apply this method of control in the westside forests of the Sierra Nevada in California where epidemics of the western pine beetle are characterized by sudden outbreaks in trees of good thrift. Trees of poor thrift do not seem to contribute to the development of these infestations, which are probably more dependent on large beetle populations developing in windfalls, fire-killed, drought weakened or *Ips* top-killed trees.

Heavier cuts, of 35 to 50 per cent of the stand, based on the writer's classification of susceptible tree types and including all trees of high risk have been made quite generally through the ponderosa pine type of the Pacific Northwest. These cuttings, which have become the standard cutting practice for the region, have proved similarly effective in reducing bark beetle damage.

Following the pronounced success of silvicultural control of the western pine beetle, there was a strong demand by timber owners and foresters for similar cultural methods of control for other bark beetles. But before progress could be made on cultural methods, it was necessary to determine whether silvical conditions of trees and stands were dominant in the development of a bark beetle outbreak. If other factors were dominant, then we could not hope for success with silvicultural control methods. Only a start has been made on this fundamental research.

To expect success from cultural control, the remedy must be directed toward eliminating or modifying the primary predisposing causes of outbreak conditions. The more important contributing silvical causes of outbreaks can be grouped in the following four categories.

Outbreaks mainly dependent upon build-up of populations in:

- (1) Recently killed trees, such as windfalls, snowbreaks, felled trees, or slash.
- (2) Stands weakened by drought, disease, or insects.
- (3) Individual trees of low vigor, poor thrift, and old age.
- (4) Stands which are overage, excessively dense or stagnated.

(1) OUTBREAKS PRIMARILY DEPENDENT UPON BUILD-UP OF LARGE POPULATIONS IN RECENTLY KILLED TREES, SUCH AS WINDFALLS, SNOW-BREAKS, FIRE-KILLED, FELLED TREES, OR SLASH: Almost all bark beetles breed freely in this kind of host material, selecting their normal host trees and the portions of trees they prefer to attack. If this killed material is abundant, outbreaks in living timber frequently follow.

Primary, aggressive species of *Dendroctonus*, *Ips*, *Scolytus*, *Pseudohylesinus* and others often develop outbreaks which can be traceable to windfalls. Even some of the so-called secondary species of bark beetles in various genera may sometimes breed in such numbers in abundant slash, broken limbs or fire-killed trees as to offer a threat to neighboring stands.

Notable examples of outbreaks developing from windfalls are the recent tremendous outbreaks of the Engelmann spruce beetle *Dendroctonus engelmanni* (Hopk.) in Colorado, Idaho, and Montana; the Douglas-fir beetle *Dendroctonus pseudotsugae* (Hopk.) in western Oregon; the western pine beetle *Dendroctonus brevicomis* (Lec.) in some early epidemics in California; and *Ips* attacks throughout the West.

Since epidemics in living timber are likely to develop from population build-up in killed trees, the obvious answer is the prompt salvage, disposal, or treatment of this material before broods can develop and emerge. In most of these situations, the silvical condition of the residual host trees and stands is of secondary importance, and yet there is evidence that in most of these situations, stand conditions have played some part.

(2) OUTBREAKS DEPENDENT UPON BUILD-UP OF BEETLE POPULATIONS IN STANDS WEAKENED BY DROUGHT, DISEASE, OR INSECTS: Severe droughts, at times, affect the health and vigor of large areas of forests. All trees in the stand are affected to some extent and become easy prey to bark beetles. One of the first observations of this factor was made by Felt (1914) who noted that the hickory bark beetle *Scolytus quadrispinosus* (Say) was favored by drought—an observation which has been confirmed by several workers since (Blackman, 1924; Craighead, 1925a; and St. George, 1929, 1930). Similarly, outbreaks of the southern pine beetle *Dendroctonus frontalis* (Zimm.) in the South (St. George and Beal 1929), *Ips* outbreaks in pinyon pine in the Southwest and the western pine beetle in California and Oregon have frequently been associated with droughts.

Tree diseases often weaken individual trees; and sometimes whole stands may be affected. For example, recent epidemics of needle cast fungus (*Elytroderma deformans*) in southern Idaho so weakened extensive stands of ponderosa pine as to lead to an epidemic of the western pine beetle.

When timber stands have been badly weakened by drought, disease, or insects, foresters and entomologists are almost helpless to save such stands from subsequent bark beetle damage. If stands have been previously thinned or the competition from associated brush and trees reduced to a minimum consistent with good forestry, stands may be in better shape to withstand periods of reduced vigor, but may not escape altogether. About all that can be done is to salvage the merchantable trees and pray for a return to normal conditions. If the weakened stands represent a more or less temporary condition, direct control to hold down beetle populations until the stands recover their normal resistance may be appropriate.

(3) OUTBREAKS MAINLY DEPENDENT UPON INDIVIDUAL TREES OF LOW VIGOR, POOR THRIFT OR HEALTH AND OLD AGE: Outbreaks of the western pine beetle *Dendroctonus brevicomis* (Lec.) in the interior ponderosa pine type are typical of this situation. Except under highly epidemic conditions, this beetle thins stands of the over-aged, poor thrift, poor health trees, especially where deficient moisture, stand stagnation, and competition have weakened the trees. In these situations, this beetle makes a selective "cutting from below" of the more susceptible trees. This tends toward the creation and maintenance of an uneven-aged forest. The successful control of this beetle, already mentioned, is due to its selective habits.

Other bark beetles which seem to operate in a similar manner are the Jeffrey pine beetle and the southwestern pine beetle. Their endemic infestations are persistent year after year, confining activities to trees of poor thrift.

For control of beetles which select individual trees of high risk, sanitation-salvage logging can be considered as the most appropriate solution.

(4) OUTBREAKS LARGELY DEPENDENT UPON STAND CONDITIONS OF OVER-AGE, EXCESSIVE DENSITY, OR STAGNATION: Some bark beetles appear to be attracted to forest stands which are overcrowded and hence are showing signs of slow growth and stagnation, or to stands which have reached a certain "entomological rotation" age. Epidemics in these stands do not concentrate on individual trees of high risk, but attack large groups of trees of all degrees of thrift. In such cases, parts of the stand, rather than individual trees, are of high risk. Attempts to risk-rate individual trees have had very little success under such conditions.

The best example of this type of group selection is the work of the mountain pine beetle *Dendroctonus monticolae* (Hopk.) in lodgepole and western white pine stands, and in young ponderosa and sugar pine stands of even age. Lodgepole and western

white pine stands are relatively immune to mountain pine beetle attack for the first 50 years. Then they become increasingly susceptible up to 100 years of age. From 100 to 150 years of age they are extremely vulnerable to being swept by a mountain pine beetle epidemic, which will leave only a few highly resistant individuals to act as seed trees for the new stand. Hopping and Beall (1948) found a relation between diameter and susceptibility. They found that "practically no attacks occur on trees below 5 or 6 inches in diameter. For every inch above this, there was an increase of approximately 5 per cent in the proportion of trees attacked." Since diameter and age are related, this also can be taken as an age association. They also found that once an epidemic is underway, "susceptible trees appear to be the dominant and more vigorous ones."

In young ponderosa and sugar pine stands, outbreaks of the mountain pine beetle seem to be encouraged by excessive stand density, the presence of understory (intermediate and suppressed) trees, and general stand stagnation due to severe competition (Clements, 1953). Susceptibility increases with age at about the same rate as in lodgepole and western white pine stands.

While the mountain pine beetle frequently makes "group selection" or "clear cuttings" in young evenaged stands of pine, its role in the mature mixed sugar pine stand of California and southern Oregon is not clear and requires further study before any method of silvicultural control can be safely recommended.

The Black Hills beetle *Dendroctonus ponderosae* (Hopk.) of the Rocky Mountain region behaves in much the same way in attacking large groups of ponderosa pine. The work of these beetles also tends toward the formation of evenaged stands by groups. During endemic periods it is hard to find and breeds in only a few weak, understory trees. When it becomes epidemic, it builds up its populations quickly and attacks large groups of trees of all degrees of thrift, apparently showing no selection. Recently, Mogren (1956) found that the largest, thriftiest ponderosa pine in the stands — trees occupying a dominant position in the forest canopy and manifesting the greatest current diameter growth — showed some degree of resistance, but during epidemic conditions few trees withstood beetle attack.

Since stands rather than trees are the units to be dealt with, silvicultural treatments might consist of thinning stands to prevent stagnation and overcrowding and clear cutting stands which are in excess of the entomological rotation age. Some success in protecting stands from attacks by the mountain pine beetle has been obtained by thinning, either taking out the larger merchantable crop trees or thinning from below and taking out trees of suppressed or intermediate crown class. Clear cutting on a short rotation obviously should be effective in depriving the beetles of trees to attack. These measures cannot be considered as beetle control measures but as desirable forest management practices to prevent or lessen beetle damage.

(5) OUTBREAKS WHICH DEVELOP IN PERFECTLY NORMAL, HEALTHY TREES: A fifth category should be mentioned, for sometimes it seems that bark beetle outbreaks do develop in perfectly normal, healthy trees. There are two possible explanations for such an occurrence (1) that the bark beetles have bred in killed or weak trees, as in the first and second categories above, and developed sufficient numbers to be the aggressors, or (2) that healthy trees are actually the preferred hosts.

We know that when large populations have been developed, bark beetles become the aggressors and few trees can resist their attacks. In such cases strong healthy trees will be taken as well as weaker trees. Outbreaks of the spruce beetles, the Douglas-fir beetle, the mountain pine beetle, the Black Hills beetle and others are typical aggressive beetles when bred to epidemic numbers.

But sometimes, apparently healthy trees are attacked and killed in the absence of epidemic conditions and it looks as though beetles had selected the healthy trees by preference. Such cases need to be critically studied. It is the writer's opinion that if all the facts were known, some predisposing tree condition would be found, and that no beetle in its right mind will prefer to attack a perfectly healthy tree.



## HOW FAR HAVE WE GONE IN APPLYING SILVICULTURAL CONTROLS?

Silvicultural control of bark beetles in the United States has only been successfully developed for a few species, of which the western pine beetle furnishes the best example. Control of this species through sanitation-salvage cuttings has been so successful that it has replaced all forms of direct control in all but a few specific situations, such as in park, recreational areas, and areas inaccessible to logging. Similar methods are applicable to bark beetle species having similar habits, such as the southwestern pine beetle and the Jeffrey pine beetle. But for most bark beetle species, little or no progress has been made in developing silvicultural control methods.

For a few bark beetle species, we have some leads as to the types of trees or stands that are most susceptible to attack, but methods of control using silvicultural tools remain to be worked out.

For a large number of bark beetle species, outbreaks are only known to occur as a result of some forest disturbances, such as fires, wind-throw, or cuttings. If such disturbances can be avoided, beetle damage will be prevented. If not, then prompt salvage of damaged or weakened timber or direct control measures should be applied. No silvicultural system or practice can hope to prevent all damage resulting from accidents of nature.

In the management of most of our wild forest lands in the United States, we as yet are applying only primitive forms of silviculture on an extensive basis. Until forest management becomes more intensive and localized we can hardly expect to meet all of our bark beetle problems with silvicultural tools. When we approach the point of practising "forestry by the acre" as is done in parts of Europe, then we should be in a position to deal more effectively with bark beetle damage.

## WHAT REMAINS TO BE DONE

Silvicultural control is often mentioned as the ultimate solution of forest insect problems, but this solution is far from being realized. Much basic knowledge still needs to be uncovered as to the role of various bark beetles in the ecology of forest stands. What primitive forms of silviculture are the beetles practising? What conditions are favorable to beetle build-up and which are unfavorable? What constitutes susceptible and resistant trees and stands? What needs to be done to increase or protect natural control agents? What will be the effect of forest practices on the biotic balance?

When these and other important questions have been answered, it will then be possible to apply silvicultural treatments with confidence that they will make forest stands most resistant to beetle attack, and not create upsetting disturbances. There is promise that when we know more about beetle behavior and preferences, we will be able to manage forest stands so as to avoid a great deal of bark beetle damage.

Even with the best that man can do, there will still be windstorms, lightning, fires, and droughts which will be conducive to creating bark beetle outbreaks. We will not be able to abandon all direct control measures, but silvicultural control should make the future use of direct measures the exception rather than the rule.

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## DISCUSSION

R. E. BALCH. Could you give us examples of bark beetle outbreaks that have resulted from weakening of trees by insect damage — particularly defoliation? Has spruce budworm defoliation of Douglas-fir initiated outbreaks of the Douglas-fir beetle?

F. P. KEEN. Outbreaks of the Douglas-fir beetle followed defoliation by the Douglas-fir tussock moth in the Colville National Forest of northeast Washington in

1930 and outbreaks of the spruce budworm in eastern Oregon in 1954. Western pine beetle outbreaks in the Klamath Indian Reservation of Oregon appeared to have increased following defoliation by the pandora moth in 1923-1925.

G. H. PLUMB. Is there any evidence that present cultural methods are furthering damage by root rots, hence bark beetle attacks on these trees?

F. P. KEEN. While root rots are often associated with bark beetle attack, I know of no evidence showing that cultural methods have increased this damage.

J. S. YUILL. In ponderosa pine, do high risk trees produce more individual beetles than low risk trees?

F. P. KEEN. Data are conflicting on this point. Some studies in northeastern California showed higher production of beetles from high risk trees than from low risk trees, while counts on the west side forests of California showed no difference.

# Engelmann Spruce Beetle Control in Colorado

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## ABSTRACT

A devastating outbreak of the Engelmann spruce beetle, *Dendroctonus engelmanni* Hopk., developed during 1941-50 in the White River National Forest in Colorado following an extensive blowdown of Engelmann spruce in 1939. After killing most of the merchantable-sized Engelmann spruce on one-half million acres, the beetle spread to adjacent areas in 1948-49. Chemical treatment of 1,219,300 trees by the U.S. Forest Service at a cost of over 3 million dollars from 1949-52, aided by natural control factors, controlled the outbreak. By 1953 the insect had killed 4,000 million board feet of spruce and 500 million board feet of lodgepole pine.

Another outbreak developed in southwestern Colorado on the Uncompahgre and San Juan National Forests following a blowdown of Engelmann spruce in 1950. Upon discovery of the outbreak in standing trees, control action was started by the Forest Service in 1953 and was completed in 1955. Approximately 127,000 infested trees were logged and 408,000 trees were treated with an emulsion of ethylene dibromide. The cost of this project was nearly 1½ million dollars.

Research started in 1944 determined that (1) the insect has a 2-year life cycle, (2) ethylene dibromide and orthodichlorobenzene are effective insecticides, (3) woodpeckers are important natural enemies, (4) parasitic nematodes reduce egg laying, (5) lethal low temperatures occasionally occur, and (6) parasitic and predacious insects and mites are common.

The severe outbreaks are attributed to the Engelmann spruce forests being extensive, mature and overmature, unstable, and highly susceptible to windthrow. While endemic losses are high, natural factors prevent major outbreaks except following heavy windthrow.

In order to clarify the method of controlling these outbreaks, the results, and some of the events, I shall present: (1) a brief review of the life history and habits of the beetle; (2) silvical characteristics of Engelmann spruce; and (3) history of previous outbreaks as recorded by Hopkins, and from my observation in some of the existing stands. Following the presentation of the story of the control program, I shall summarize some of the research results that had an important bearing upon the two control operations and upon the future management and protection of Engelmann spruce in Colorado.

As described by Massey and Wygant (1954), the beetle has a 2-year life cycle. Soon after snowmelt in the late spring and early summer, the adults emerge from hibernation and attack green trees. The flight usually commences in mid-June, reaches its peak in late June or early July, and ends in late July. The insect overwinters in the immature to mature larval stage, completes development to adult stage in August or September of the following year, and hibernates the second winter in the bole or base. The following spring the new generation attacks green trees in the surrounding area.

Engelmann spruce in Colorado grows at 9,000 to 11,000 feet elevation in a cold, humid zone, often in association with subalpine fir. It is a long-lived tree, maturing in about 300 years. Under favorable conditions it will average 18 to 30 inches in diameter, 80 to 100 feet in height, and 25,000 to 40,000 board feet per acre in yield. Most of Colorado spruce stands are virgin, with few roads into them.

Hopkins (1909) reports evidence of devastating outbreaks in several areas in Colorado about 1875. Observation of the author in some of the immature spruce stands indicate that a number of outbreaks also occurred prior to those reported by Hopkins. No records are available as to cause of the early outbreaks. The recent ones developed from windthrown spruce, which the beetles prefer to infest. In the down trees, the brood is protected from predation by woodpeckers by the winter snow cover. As a result, populations build up and kill many standing trees in all vigor classes before

woodpeckers and other natural factors bring about control. The two control projects mentioned previously were organized with the assumption that chemical and logging control would destroy the major concentrations of beetle populations until woodpeckers and other natural enemies increased. Such proved to be good strategy, for three species of woodpeckers — the Alpine three-toed, the Rocky Mountain hairy, and the downy — along with physical and other biological factors soon gained complete control. Once the balance was tipped by chemical control, the decline of the outbreaks was rapid.

On the White River National Forest, the outbreak spread to adjacent areas after the local food supply was exhausted and threatened to destroy other major bodies of spruce in Colorado. The beetles flew 16 to 30 miles across non-forested areas to establish new outbreak areas. Control operations were launched promptly in these areas in 1949-50 to wipe out the new positions. By 1952, the new outbreaks were controlled, partly as a result of unusually low temperatures in 1951.

A second and independent outbreak developed in southwestern Colorado from a blowdown in 1950. Upon discovery of the outbreak in standing trees in 1953, control was promptly organized by the Forest Service to prevent the spread to other areas. The first step was an orderly survey (Knight *et al.*, 1956) to determine number and location of the infested trees and to locate roads into the area. Plans made during the fall of 1953 called for chemical treatment of 189,000 infested trees and logging of approximately 33,000 others during the summer of 1954. The estimate for 1954 was based upon the number of infested trees in 1953 plus a projected increase of 3 to 1 over the 1952 trees. The increase as determined by the 1954 survey was three times that predicted, or 9 to 1.

Time does not permit a detailed description of the techniques of treatment nor the many complications arising from employment of large numbers of workers, housing and feeding them, the construction of many miles of new road to reach the areas, inclement weather, and the purchasing, mixing, storing, and transporting of the insecticide, all during a short work season of June 15 to October 15. The trees were spotted and individually treated with insecticides. A hand-operated bucket sprayer equipped with a No. 6 solid-stream nozzle was used. Insecticide could be effectively applied to a height of 30 feet. Accomplishments and data as compiled from several Forest Service reports on each of the two projects are as follows:

	1949-1952 <sup>1</sup>	1954-1955 <sup>2</sup>
Total trees chemically treated	1,219,344	407,961
Total trees cut for logging control	<sup>3</sup> 5,027	<sup>4</sup> 127,000
Grand total infested trees treated or logged	1,224,371	524,961
Acres on which treating was done	33,300	22,403
Total gallons of insecticides used	<sup>5</sup> 1,691,296	<sup>6</sup> 1,182,643
Total man days	82,140	60,000
Total cost	\$3,327,946	\$1,475,338
Miles of road constructed	421	129
Miles of roads improved and maintained	125	126

<sup>1</sup> On White River, Arapaho and Routt National Forests.

<sup>2</sup> On Uncompahgre and San Juan National Forests.

<sup>3</sup> These were uninfested trees cut prior to flight to trap beetles.

<sup>4</sup> Does not include an unknown number of uninfested trees felled for trapping beetles.

<sup>5</sup> Insecticide was 8 pounds of commercial grade orthodichlorobenzene dissolved in fuel oil to make 5 gallons (Massey and Wygant, 1954).

<sup>6</sup> Insecticide formulation was 3 pounds of ethylene dibromide, 8 ounces emulsifier and fuel oil to make 1 gallon. This 1 gallon stock solution was then added to 4 gallons of water (Massey *et al.*, 1953).

The control projects could not have been successful without the assistance of natural enemies, nor would the operations have been undertaken without the knowledge of their habits, although fragmentary, and some assurance that these enemies would take over and complete the suppression of the outbreaks.

Woodpeckers were the most obvious and important agents. Their numbers increased to 9 per acre or more in heavy outbreak areas (Yeager, 1955). The three species resided yearlong in the infestations, often consuming all of the Engelmann spruce

beetle larvae above snowline. Woodpeckers preferred to feed on the uppermost part of the infested stem. They usually consumed the insects above the maximum height of spray application, thereby supplementing the chemical treatment. Concurrent with and following these control operations, numerous outlying and localized outbreaks were greatly reduced by woodpeckers. In short, every effort was made to make maximum use of woodpeckers and to avoid competition from chemical control.

The Engelmann spruce beetle is well adapted to survive the normal low winter temperatures. Laboratory tests showed that subcortical temperatures of  $-25^{\circ}\text{F.}$  to  $-30^{\circ}\text{F.}$  are lethal to larvae and that  $-15^{\circ}\text{F.}$  kills adults during midwinter. An unprecedented cold wave blanketed Colorado on February 1, 1951, during which temperatures as low as  $-56^{\circ}\text{F.}$  were recorded in the valleys of the outbreak areas. The low temperatures killed approximately 75 per cent of the larvae. Survival was largely limited to the larvae and adults in bases of stems beneath the snow.

Massey (1956) found the beetles to be heavily infested with two species of parasitic nematodes (*Aphelenchulus reversus* Thorne and *Sphaerularia dendroctoni* Massey). Parasitism was as high as 75 per cent in individual trees and 35 per cent average of all trees in some areas. He found that female beetles infested with *S. dendroctoni* laid an average of 29 eggs; and uninfested females, 77 eggs. Female beetles infested with *A. reversus* laid 35 eggs; and uninfested, 63. The value of these parasites in the overall suppression of the beetle is not yet fully understood.

Toward the end of the first control project, a braconid parasite, *Coeloides dendroctoni* Cush., became numerous. Although its effectiveness is limited by the bark thickness of trees containing its host, it may be an important factor in the rapid decline of some outbreaks. Its numbers did not increase significantly during the second outbreak, possibly because of its short term.

Up to the time of the recent beetle outbreaks, little of the Engelmann spruce in Colorado has been harvested, largely because of high production costs and inability to compete with forest products produced from more accessible stands. The Forest Service realized that this position would change and strategically proceeded to preserve this potential timber supply. Furthermore, past history shows that major Engelmann spruce beetle outbreaks are infrequent. The control projects were emergency measures to preserve the spruce volume until more roads are constructed and the stands can be placed under management. Progress in that direction is rapid because of the favorable market for Engelmann spruce for lumber. In this orderly harvest and eventual development of intensive management, certain practices and measures will be helpful in prevention of excessive beetle-caused losses. These are:

1. Close and continuous surveillance for abnormal amounts of windfall that might develop outbreaks. This will require the help and coordination of all foresters to ensure complete annual coverage of the spruce forests. In addition, an annual insect aerial survey by trained observers will provide helpful added insurance against large outbreaks.

2. Harvest should commence with the overmature stands, for in these stands endemic infestations and blowdown incidence are highest.

3. The cutting system should be designed to hold the incidence of blowdown to the minimum, whether the cutting system be a light selection, clear-cut in groups, or clear-cut in strips.

4. Prompt salvage of abnormal blowdown.

5. Greater use of trap logs for curtailment of beetle populations.

6. And last, but not least, a research program to learn the details of the natural control factors so as to know how and when to depend upon them to the maximum extent, and to develop a more economical chemical control method that can be used upon infestations not responding to the natural control factors.

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## DISCUSSION

H. A. RICHMOND. In relation to the Engelmann spruce beetle in blowdown, what significance do you place on snow as a protective blanket which would safeguard the overwintering beetle from woodpecker feeding?

N. D. WYGANT. Since woodpeckers are not migratory birds, they must have a yearlong food supply to increase in numbers. The winter food supply probably determines their numbers; therefore, they do not become a controlling factor until the outbreak goes into standing trees. By that time the beetles may have multiplied greatly and have become uncontrollable by woodpecker alone.

F. P. KEEN. Do you attempt to treat 100 per cent of the infested trees? In the early days of bark beetle control, Dr. Hopkins thought it was necessary to treat only a proportion (say 80 per cent). I believe experience threw doubt on this.

N. D. WYGANT. Treatment of 100 per cent of the infested trees within the control units was attempted, but we know the goal was not attained. We were aware of Hopkins' theory and the results. But that work was against another bark beetle, which is not as heavily preyed upon by woodpeckers. Treatment of infested Engelmann spruce was geared to the abundance of woodpeckers within the area; therefore, the combined effect approached 100 per cent. Many trees and areas were passed by for chemical treatment where woodpeckers were adequate to cope with the beetle.

J. B. THOMAS. Was the chemical control effected through killing of larvae in the trees by a fumigant effect or by contact killing of emerging adults?

N. D. WYGANT. By fumigant effect and possibly by penetration and contact soon after application. The insecticides had little residual value.

R. F. SHEPHERD. You state that the beetle flew from White River to adjacent areas; do you have any additional information on beetle flight?

N. D. WYGANT. Studies have been made by R. H. Nagel and J. N. Davis through the use of radioisotopes. The manuscript for publication of their results is now being prepared.

GEORGE H. PLUMB. Were any trap trees treated with a contact insecticide at the time of placement to kill the beetles as they attack the trap logs? If so, did the insecticides used exert a repellent effect?

N. D. WYGANT. Logs sprayed with a 2 per cent emulsion of DDT are not infested. We do not know whether the DDT kills the beetles or repels them. We suspect the latter. R. H. Nagel is testing several insecticides with the hope of developing a chemical trap log that will not repel the beetles.

J. S. YUILL. Do you have any leads as to practical means for increasing numbers and effectiveness of nematode parasites?

N. D. WYGANT. C. L. Massey is continuing his studies of nematodes parasitic upon and associated with this and other species of bark beetles. As yet, he has no significant leads in that regard.

# Trends in Forest Management in Eastern Canada and the Relation of these to Control of Forest Insects

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## INTRODUCTION

My remarks today have to do with trees and with the attitudes of persons interested in using the trees before they are destroyed by insects. If these words seem to refer repeatedly to spruce budworm please assume that they are meant to apply to any important local forest insect.

Because I am unable to do so neatly, I shall not try to define "Forest Management", not even for Eastern Canada. Some of my acquaintances talk about and write about forest management and succeed in moving it completely out of the forest without ever saying just what it is. Two versions of the concept of forest management, however, I must mention to you because they are very extreme opposites and therefore the probability of either being true is very slight. Occasionally you will find a forest user who considers forest management, at any given time, to be the happy marriage of forest with his business regardless of how the business affects the forest. Not so rarely, and I must say that these are almost invariably landless souls and usually of a studious nature, do you find those who think of it as a scientifically planned and regulated vegetable and animal Utopia and you can sometimes sense that they would like to be around the scene on that great arrival day. This group considers the actions of the forest user as something akin to rape and puts up with them reluctantly. I can say this lightly, having at one time or other been in each camp. I believe my own idea of what forest management means wallows around well within these extremes, veering at the moment slightly toward the second coming of Paul Bunyan rather than toward the Utopian millenium.

## CANADIAN FOREST BUSINESS

In discussing the present forestry scene I believe, in fairness to some here today, I should say a few words about the country and its history of forest use. You have only to fly over this land to know that it contains comparatively few persons and a great host of trees. The continuous stretch of forest, mainly coniferous, is impressive. The human population, always small, is growing at a great rate but a recent shift away from the land closer in toward cities and towns belies this growth except in the crowded urban areas. The forest country is, practically speaking, a human wilderness.

Very early in the days of settlement on the land, men began to find out how to wring an easier living from the forest than from the clearing.

A thriving trade developed in forest products between this new country and the outside. It began with the great fur trade. The first wood products to be exported were masts and spars. Wooden ships, some of which were built here for the export of Canadian goods, carried hewn timber squares, mainly of pine but some of birch, to the British market. Half way through the last century, the business was in wide-faced, thick, sawn deals of pine and spruce also mainly for Britain. From 1880 to 1920, lumber was king of the forests products. It is still important, today, although first place is being taken over by pulp and paper. For some years, there has been a trade in other lesser products, notably in peeler logs and pitwood. Practically all these products have been extracted from the coniferous or softwood forest. Fuelwood, formerly so badly needed to keep us warm through the winter, provides the exception and uses hardwoods where these are obtainable.

The business in forest products has, as you can tell, had its face lifted several times, usually by forces and demands from outside Canada. Its strong export features have not changed and today, as in former times, it is regarded as one of the great bulwarks in the Canadian economy. In the history of these enterprises there have been good times and poor and sometimes changes were accompanied by considerable hard-

ship. Today, we can hardly imagine a serious decline in our forest business, especially in the pulp and paper group. A sobering thought, however, is the recollection that the several exploitive enterprises which preceded it had their heyday and passed on, and in some places the decline of a once great lumber business was the direct result of changes in the character of the forest and not because of a falling off in world demand.

We are fortunate that our products find favour in these outside markets, especially the United States paper market, because we must export goods from Canada in order to live.

### CHANGES WILL BE CANADIAN

In any country, as it develops, business enterprises seem to change from simple to more complex forms. Between countries of different ages, the chronological, geographical, and many other kinds of dissimilarities make it difficult to use the experience of a particular country as a guide elsewhere. For instance, there has been no situation analogous to the changing Canadian forest and forest business of the past hundred and fifty years nor is this kind of history likely to be repeated here or elsewhere.

By extrapolation from our own experience are we most likely to gauge the form that our forest management of the future will have. Of a certainty its Canadian flavour will increase as we get older and to that extent will it be peculiar. That is not to say that we shall not borrow from the outside; we shall, but warily.

Perhaps it is a bit ironic that we first became formally acquainted with forest management in the universities which feature the theories and practices of foresters who worked in Germany and France a good many years ago and who wrote books which became text books. It is worth while to note that these two countries are wood importing countries and have from time to time been good customers of ours.

We are still young — so young and dependent that our forest management practices, such as they are, are hitched directly to the value of a cord of our wood in the market place. We may never get into the fashion of basing them on the productivity of the soil.

In our total experience, the market value of the cord of wood is high at present. It has grown irregularly from almost nothing in the lifetime of the youngest pulpwood trees and middle-aged pulpwood cutters. When business was poor, the value was almost entirely in the work done on the trees to change them into piles of wood. Once or twice in my memory, it slipped still lower. Today, standing trees have a real value and if it is high enough, one can perhaps afford in the scheme of management to protect them just a little bit. Wood value is used by traders and taxers and, to a great extent, it determines what takes place in the forest — call it forest management or by any name you wish. When the value shrinks to zero, forest management is reduced to theory. One other thing about this forest value: locally it is different for different persons in different places at the same time and may be greater than the general market price to you if you sorely need wood in your business.

I believe the growth in value of the coniferous forest in this country provides the reason for trends in changing attitudes towards that forest which are discernible today.

### THE FOREST STRUCTURE

What kind of forest is this which we must manage? That to which I refer stretches from the prairie to the Atlantic. Insects and disease and wind and fire lumped together have had more to do with the structure of that part of it which will be cut in the next fifty to one hundred years than has man through his cuttings. Forest operations are catching up but the four original influences are still powerful. All four are moulders of new forest, and acting singly or in combination, have a tendency to create conditions favourable to the formation of even-aged stands sometimes of single species. This has been the order in the past except in those places where none of these forces has exerted much effect for a very long time. Very important events give rise to age classes. In some stands three or more of these may occupy parts of a site at the same time. By far the most common kind is the stand containing one age group. So much is this the rule that in most instances in our forest surveys, stands may be catalogued by age classes.

Foresters and others are prone to talk about the conversion of simple forest structures such as are common here to something resembling a theoretical all-aged or uneven structure of several species in mixture. They reason that such a condition is much safer from almost any point of view and that we would not have the outbreak visitations of insects and other bad things that seem to be our lot were we fortunate enough to have a different kind of forest. Certainly it would be interesting to find out if this reasoning holds up in practice. But for us, here, and now, the point is more or less an academic one since we do not know of any way to bring about the changes. The nature of the forest itself indicates that in youthful stands conversion of stand structure is an impossible task and there is no point in trying such changes later on. Whenever stands break up naturally and there is a semblance of the all-aged condition present, there is also present a high degree of overmaturity. Probably in our time, no big change will take place in the overall structure of the softwood forest nor in its species composition though the area of fire type forest may grow in extent either by accident or by design.

This has been the milieu of unnumbered insect outbreaks in the past, especially of the spruce budworm. There seems to be no good reason to assume that these will not recur when conditions are favourable.

### NEW FOREST MANAGEMENT TOOLS

Those of us who can go back in memory thirty-five or forty years have seen some remarkable changes come to our forest and to forestry. Then forest management was a course we took in school. There were perhaps two forest entomologists working on spruce budworm. Travel was by foot overland or by canoe. The forest was almost as much an unknown as it was a hundred years before. We have seen the hunt for good logs change to the cutting of stands of trees and these in some recognizable order. We remember how it was that the forests came to be mapped and counted for the first time, so that the new kind of cutting could be controlled. No matter that the bits and pieces of information did not find their way into a national inventory — the information so gathered was useful and was used. Canadians were among the first to improve their forest maps and estimates of timber through the use of aerial photography. We are still finding new uses for this forestry tool, some of which are of interest to the entomologist. The flying machine, as it was called in the beginning, has developed into a very important survey aid; in fact, in some places, it has become indispensable to the forest manager. From it, he can view directly woods operations, fires, insect feeding, and by using it, to commute from place to place, oversee much of his work programme. Aircraft shall become even more important to us in future forest tasks.

The crawler tractor should have been invented by a woodsman because he needed it so badly. We were late to see its application in the bush, but have made up for this by building in the last twenty-five years thousands of miles of forest truck road. More than anything else, this coming of powerful earth moving equipment to the forest has changed our situation. Now it is possible in a single season to manoeuvre into an entirely new operating position if necessary.

If one adds to this list herbicides and insecticides which have been synthesized since the war, some idea of the difference between then and now in the ability of the forester-manager to act in an emergency may be realized.

### DISCERNIBLE TRENDS

Hand in hand with the availability of new and powerful aids to accomplishment of work is an apparent increased interest in projects which may be called "short run" or that are said to be of "a practical nature". This seems to be evident amongst Canadian foresters regardless of what one reads about forest management theory. The situation, if true, must horrify some. But it seems to me to be the natural way to meet events which take place in our forest without apparent order or reason. In my opinion, this is no time to be slowed down in our development of forest management by long run planning based upon assumptions which pass for facts. Not that such planning is wrong per se, but because the forest situation seems to call for a different approach. In many parts of our large forest region, men are trying many things for the first time without



any idea that they are contributing to the future of forest management — the future theory no less! A healthy thing involving foresters and biological workers of all stripes!

A trend in forest management which has struck me forcibly is the approach to a really free trade in ideas and information. This is noticeable between units of Industry and between Industry and Government. This tendency to do business with neighbours has created an arena in which differences may be thrashed out and agreements reached. Cooperative forestry projects now in process are examples of how far the trend has progressed.

A present day tendency is to separate the forest management of the settled part of the land with myriad small forests and owners from the large hinterland composed mainly of crown owned forests and to admit that these will be handled in different ways. I wish that those who are forever comparing these two forest systems would explain the limits between which such comparisons are useful and valid. In my opinion, these two are not comparable in terms of forest management, and I believe the yield figures which are being used are phoney. The spread of the tree farm movement is an example of this trend. The name "tree farm" is an apt one for a small piece of domesticated forest which is being intensively looked after by the owner.

Perhaps the most important trend in our thinking is reflected in the attention which is now being focused on forest time. We have considered that trees have form and mass and locale but rarely have we considered them in a "for how long" way. Men who cut volumes of wood from stands of trees and deliver these to a plant in a business system that is hedged in and around by calendar deadlines or which must squeeze itself into a year of unpredictable seasons may be forgiven for dropping this dimension.

In the past few years, we have noted the work done by several commissions on Forestry (four Provinces) and now we have one set up by the central government whose job it is to conjure up a picture of Canada's short-term economic future. It is hard to imagine these completing their tasks without considering this aspect of forests and forestry.

Industry, at this time, also must be giving close attention to forest time as it studies expansion of plant or the building of new units of production.

The idea that some forestry tasks become so heavy at times as to require financial and other kinds of help for those engaged in them is being accepted. The Canada Forestry Act may be cited as a tacit admission by the central government that it believes it has responsibilities in the management of Canadian forests. The admission has been a long time coming and the kinds of help most needed have not been forthcoming as yet, but there are signs of change.

These are not the only signs that forestry is alive and changing. The utilization of all tree species is a dream but it is a bit closer to being realized today than ever before. So is the utilization of more of the tree.

A long look is being taken at our record in protection, chiefly protection against fire. As you perhaps know, the incidence of wildfire has gone up with increasing opening up of the wilderness by new roads. That the fires, most of them, are small is an indication of real improvement in the ability to get to the scene in time to quench it. In spite of the educational programmes designed to change the careless and the ignorant into good forest citizens, we have not succeeded in damping out those who play with fire nor can we hope to be completely successful in doing so. We shall, in future, of necessity concentrate more on destroying fuel for fire and upon fencing woods travel out of areas of high hazard. I believe in the adage, "If you can't fight 'em, join 'em". Before long, I think we shall be fighting fire with fire, not only to make the forest a safer place but to bring back in some places the kind of forest on which some of the business is based. In order to obtain regeneration where burning does not provide it, the airplane will do aerial seeding at the proper time.

In fir-spruce forests of the kind which are knocked about by spruce budworm, we have a real dilemma. It is difficult to see in any variation of the cutting method an advantage over the system of clear cutting in use now.

In this type of forest, after tree mortality caused by insect feeding provides a fuel pile over large areas, wildfire may change the species composition in the succeeding



forest for a long time to come. About the only way to keep fire out of such a forest is to keep trees alive so that risk is high only in cut-over areas. These, while in a high hazard stage, bulk small in area in terms of the usual general outbreak aftermath condition and may be treated to prevent fire.

### FOREST MANAGERS' POLICY

It is an oversimplification to say that the forest manager is doing a good job if he succeeds in carrying out the following tasks:

1. Cutting the forest as near to the time of ripeness as he dares.
2. Seeing that regeneration is adequate by the time of cutting or providing it promptly after cutting so that the land does not idle.
3. Protecting his own interests and those of others against all forms of damage to forest stands wherever this seems to make sense.

Very, very easy to say but very complicated and difficult to carry out in practice. To make the best decisions, he needs good, new information. Not many regional or national surveys are of much use to him. He should have his own much finer in tooth. There are exceptions of course. In lieu of something better, he will always be glad to have those vital statistics and the address book of forest insect pests compiled yearly by the National Forest Insect Survey. Always is he looking for help from the forester, entomologist, pathologist, engineer — to name only a few. It is necessary for these to remember that the manager cannot always do what they would have him do — that usually in Canada he is part of a business enterprise in which a chunk of forest is an integral part of the business.

### FOREST MANAGEMENT TRENDS AND INSECT CONTROL

Let me say here that the changes mentioned have worked out as much to the advantage of the forest entomologist and pathologist as to the forester, and some of the powerful working tools available today are just as important to one as to the other.

*The times have placed us in a position from which we can oppose a forest insect scourge.* That we do know. Certainly we had to do some work to find out this much.

I shall digress at this point and tell briefly of the projects with which I have been connected for the past five years. Down East the budworm has not created much stir until this present outbreak. It did extensive and serious damage in my memory and this reputation for upsetting the forest more than anything else decided the course of protective action in New Brunswick in 1951.

Those who undertook that first forest spraying project knew of the earlier damage and were fearful — fearful that the forest on which an enterprise was based was going to die. They realized what others since have found out — *for the first time, part of a Canadian forest based business is competing with an insect for the same woodpile.* There was some short run planning needed and a making up of the mind in a hurry.

In 1952, and each year since, forest spraying operations have been carried on. The new tools have been used — air photo, tractor, truck, radio, airplane, insecticide and others. Roads and airstrips were built; materiel was portaged during winter months; spraying operations were observed directly from aircraft and their supervision made easier through the use of radio. None of these things could have been done in 1917.

I have a few numbers which indicate the scale of the work. Since 1951, seventeen flying bases have been built in northern New Brunswick and Gaspé and about 16,000 tons; i.e., over 4 million gallons of insecticide, have been sprayed on almost 8 million acres. About eight million dollars have been spent on the work thus far. In size, these operations are of the same order as the annual projects in the Pacific Northwest United States between 1949 and 1955. We have borrowed quite heavily from U.S. experience wherever it seemed fitting, especially in the first year.

I wish we could report results of spraying as clear cut and complete as theirs. It seems, in their case, that an outbreak has received a knockout blow and a forest has been saved.

Our work has come in for its fair share of criticism — favourable and adverse. Some think the treatment is too rough to tolerate; others that we are interfering with

nature. Some think we can only make matters worse. I have noticed two things about those who speak against:

They favour some other project on which they believe money should be spent first, and

They usually do not have a direct personal interest in timber values which are being threatened.

A friend of mine who shall be nameless is a case in point. He reversed himself the day after he became identified with a forest property which had come directly into the path of the outbreak and overnight became a forest spraying fan.

From a tree protection standpoint, we can say that after five years, all trees in most of the sprayed area are alive and most of the trees in the remainder of the sprayed area are alive. There are a few spots where most trees, if not dead now, are going to die and there will be more tree killing before long. Generally speaking, the results are very encouraging. But for the spraying effect, the losses by now would have been staggering, not only in mature but in younger trees as well. Areas in which trees are gone beyond recall have been sprayed too late the first time, or have been missed, or have been allowed to go too long between sprays. In most of these spots, many trees can still be kept alive by further spraying. Areas set aside by the Division of Forest Biology for biological study purposes and left unsprayed are in a dead and dying condition which may have been reached earlier had surrounding spraying not taken place. These give a conservative slant to the effect of the treatment when used for comparison.

The spray plan generally has been to move into critical areas and knock down the insect population, thereby giving the trees a chance to get some foliage back.

The insect outbreak is thriving, retaining its vigour undiminished. The question now in some minds is this—will the outbreak be able to subside as long as trees produce food for the insect? And after spraying they do grow new food for the insects. For example in an area roughly in the middle of the sprayed area there is a small bit of forest that has been given a shot of spray each year for the past five years. The trees have most of their needles and to the casual observer, appear like those outside the area of infestation.

From what I have seen of results, I am sure that it is possible to maintain large areas of forest in good condition during an outbreak period or for a long period of time. In order to do so, the trees should not be allowed to come too close to death before the first application and should perhaps be given some help, perhaps as often as every other year of severe outbreak conditions but not necessarily so.

In most of northern New Brunswick and the Gaspé region, this is still possible but will probably not be achieved except through bold measures.

Entomologists and others have had a splendid chance, for the first time in this country, to see and study what happens when a large scale man-directed defence opposes a large scale violent insect outbreak. This has been a valuable experience; for as time goes on, it will be less probable that man will remain aloof during outbreaks of insects if by acting he can profit.

Unfortunately, outside of insect and closely related studies, there has been little else of a scientific or investigative nature which has been planned in cooperation with spraying operations. There have been some investigations of a purely fortuitous nature yielding results which have been most illuminating and profitable. These could be said to be more the result of collision than planning ahead.

The projects have made those connected with them see the worthwhileness of planning and working together. Entomologists have been very busy, too busy perhaps for their own good, obtaining information on which to base plans for further operations. Some of the load of survey work perhaps should come off their shoulders so that they may give more of their time to the study of those things in which they are most interested and from which we may expect a high return in the future.

The projects have had an effect on the Canadian aviation business. In particular, one firm which has had the responsibility for assembling and maintaining spray aircraft since 1953 has gathered valuable experience which will be useful in other kinds of aerial forestry work.

Our large scale operations have leaned heavily for support upon the United States agricultural aviation business without whose existence, experience and availability, we should probably not have got started.

I have finished with the digression which has been used deliberately to point out the relation between forest management and forest insect control. I must confess to changing the title of my remarks because I do not understand the meaning of "Cultural Control of Insects". Perhaps it should have been further altered because I'm not at all certain I know what you mean by "Control of Insects".

Does the forest management action just described, in which the trees on millions of acres have had their life time extended so that it may be possible for industry to use some of them — does this add up to control of forest insects? I believe it does.

Outbreaks of spruce budworm in Eastern Canada, in my opinion, are not likely to be prevented through forest management, nor is their spread likely to be controlled by man, at least for a long, long time. Tree protection for limited areas is practical and possible today; that has been shown. What the future will require of us in this direction we do not know.

Tree protection is vital in some parts of our forest now — places where the trees are valuable and where protection will pay off. It seems to me we should be giving more thought and study to this matter than we do now. It is apparent to me that we do not know enough about the condition of trees in our forest at any time. Foresters have been slow to see that tree condition may be more important than wood volume per acre or extraction costs per unit of wood volume. I have a feeling that the condition of trees during an insect outbreak has been judged sometimes more by the course and duration of the outbreak than by direct diagnoses of tree and stand condition.

Forest management more and more will have to concern itself with tree protection in all directions as the country becomes older and the use of the forest more widespread and complex. Advances in knowledge and a better understanding of the interaction of insects, diseases and trees — particularly I think a better understanding of reactions and resistances of trees to those organisms which live upon them and also to man's protective measures, — should give us an increasing ability to control disturbances such as, for example, damage from spruce budworm.

Ability to carry out a protective action, or information indicating that such action should be taken, does not mean that steps to prevent damage will be taken in time to be of much use, or that they will be taken at all.

Just as any forest product must be sold, or a demand for it created, so has forest protection to be sold. *At the present time, not enough Canadians believe in actively protecting resource assets.* There is still a selling job to do in order to put protection in all its ramifications where it belongs in the forestry panorama in a young country such as Canada. There is small satisfaction in making plans for the future use of our forest until we can master the difficult task of protecting what we have at any time. This we have not yet succeeded in doing with any degree of surety or timeliness.

I shall terminate my remarks by saying that control of forest insect damage is a forest management problem. They are one and the same. In certain places in Canada at the present time — some of which perhaps some of you will see during your visit here — large scale crude measures are being taken to achieve *insect-damage control*. Those who are involved in the venture consider it to be the only forest management action possible under the circumstances and are very happy indeed to work alongside the specialists in forest insects and diseases in a cooperative effort to defend and maintain our forest based business enterprise.

## DISCUSSION

H. S. FLEMING. What is your opinion regarding aeroplane spraying disturbing the balance of nature, such as killing?

B. W. FLIEGER. That question could best be answered by the forest entomologists.

R. E. BALCH. With regard to Mr. Fleming's question about the balance of nature, I should point out that this will be discussed on Friday in connection with Dr. F. E. Webb's paper.



# Forest Insect Surveys in the United States

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## ABSTRACT

*Forest insect surveys in the United States are part of a broad program of work to protect the forest resources of the Nation against undue damage and loss caused by insects pests. They comprise a countrywide program activity designed to locate abnormal insect infestations in their early stages; to appraise their potential destructiveness; and to determine the needs for their control. The surveys are conducted on a co-operative basis by agencies in the Federal and state governments, and by private land-owners and timber operating companies. On the one hand, the surveys are closely related to the programs of work in forest insect research and, on the other, to the programs for direct or indirect control. The methods that are used in survey operations are variable, depending upon the objectives for which infestation information is being obtained. Tree damage or tree-killing that is caused by insect pests is located by aerial observation or by ground inspection of forest stands. After infestations have been found, their status and significance are appraised in order that a determination can be made as to the needs for their control and whether or not the proposed control undertakings will be biologically sound.*

It is a pleasure for me to appear before you here today to tell you about forest insect surveys in the United States. In the time that is available, I will try to give you sufficient background information to point up the importance of the surveys, to tell you how we are organized to conduct the work, to explain what the over-all objectives are, and how these objectives are met in a co-operative way between the states, the private land-owners, and the federal government. I hope that my discussion will also make it clear that the surveys are closely related to a broad program of work in forest insect research and to an over-all effort on the part of public and private agencies alike to protect the forests of the Nation against undue damage and loss caused by insect pests.

Before going into detail on these points, however, I want to say here at the outset that my remarks will apply primarily to forest insect surveys that are conducted by the Division of Forest Insect Research of the U.S. Forest Service. Let me add, however, that I certainly do not want to leave the impression in the mind of anyone that the Forest Service is doing all of the work in this important field. As a matter of fact, I would be remiss in presenting this subject if I failed to emphasize that a great amount of effort in surveys is also being expended by several of the states, by many of the private land-owners, by the timber-operating companies, as well as by other agencies in the federal government.

At this point, I believe it would be worthwhile for me to tell you a few things about the forests of the United States. I think you will be interested in knowing where they are located, how extensive they are, their ownership, and about their importance in our national economy.

Briefly stated, the forests of the United States constitute one of its major natural resources. They are the source of supply for a major portion of the Nation's vast needs for timber, wood, and wood products; they also are the storage basins for a large part of its usable water, the habitat for an abundance of fish and game, the summer range for vast herds of livestock, and the outdoor playground for millions of people the year around. The wood-using industries actually make up a major part of the economy in many parts of the Nation. The same is true for other businesses that are dependent upon the forests and the forest resources. It is estimated that about one person in every eight who is gainfully employed in the United States, is dependent, in one way or another, on the Nation's forests.

The forests of the United States are extensive; in fact, they occupy about one-third of the total land area in the Nation. In round figures there are some 489 million



acres of commercial forests in the United States. In addition, there are about 175 million forested acres which are either non-productive commercially, or which are reserved for municipal watersheds, National and State Parks, recreational use, or for other purposes.

Approximately three-fourths of the commercial forest land in the Nation is located in the eastern half of the country, with the greatest concentrations in the Southeast, the West Gulf, and the Lake States Regions. The most extensive forests in terms of sawtimber, however, occur in the West, in the Rocky Mountain States, and along the Pacific Coast in Washington, Oregon, and California. The forest growing stock in the Nation, including Coastal Alaska, contains about 517 billion cubic feet in live trees 5 inches or more in diameter. Nearly three-fourths of this total volume of wood is contained in trees that are large enough to be manufactured into lumber.

It is of further interest that the total area of commercial forest land in the country is almost equally divided between the two major type groups, the softwoods and the hardwoods. Almost equal areas of the softwood types occur in the eastern and the western parts of the country; in contrast, the hardwood types occur almost exclusively in the East. Another point of interest is that most of the commercial forests in the United States are privately-owned. The wood-manufacturing industries, farmers, and other individuals, own approximately 73 per cent of the forests. Of the remainder, 21 per cent is owned by the federal government, and 6 per cent is owned by State and local governments.

I would now like to tell you something about how destructive insect pests are throughout the country, and to compare their importance with some of the other natural agents which damage and destroy the forest resource. It has been recognized for a long time that insects are among the most destructive of all the natural agents affecting the forests. Outbreaks have been reported from most parts of the Nation for as long as records are available. Extensive stands of forest trees have been killed by such insects as the western pine beetle, *Dendroctonus brevicomis* (Lec.), the mountain pine beetle, *D. monticolae* (Hopk.), the southern pine beetle, *D. frontalis* (Zimm.), and the Engelmann spruce beetle, *D. engelmanni* (Hopk.), to name but a few. In addition, trees on thousands of acres have been killed or seriously damaged by defoliating insects such as the spruce budworm, *Choristoneura fumiferana* (Clem.), the Douglas-fir tussock moth, *Hemerocampa pseudotsugata* (McD.), the pine butterfly, *Neophasia menapia* (F. & F.), the gypsy moth, *Porthetria dispar* (L.), and others. Past experience has shown that all of the above species of insects not only have killed or damaged vast numbers of trees but that they, and others, also have contributed to the deterioration of forest types, to the occurrence and destructiveness of forest fires, the loss of usable water, to soil erosion, and to other types of damage in the affected areas.

Just recently the Forest Service, in co-operation with forest industry, state and private forestry organizations, and other agencies in the federal government, completed a comprehensive appraisal of the timber situation in the United States. In a publication, "A Review of the Timber Resources of America", soon to be released in final form, one chapter is devoted to natural agents which cause tree mortality, and the extent to which they contribute to the drain of timber in the Nation's forests. As a result, we now have for the first time a fairly accurate picture of the true magnitude of forest insect-caused losses.

I think it would be worth while for me to take a minute or two at this time and cite a few statistics from this Review that pertain to insect-caused losses. For example, during 1952, which was a fairly typical year, insects killed about 28 per cent of all the trees of commercial size that died in the forest of the country. This amounted to about one billion cubic feet of wood. In the mortality of sawtimber alone, insects were responsible for some 40 per cent of the total loss, or approximately 5.1 billion board feet. Furthermore, insects were responsible for an additional one billion board feet of sawtimber mortality annually in outbreaks which are so unusual that their frequency cannot be predicted. According to the Timber Resource Review, insects outranked forest fires as a cause of sawtimber mortality by a ratio of seven to one. They outranked tree diseases also, by a ratio of two to one.

With this brief accounting of the importance of insect pests in the United States, I feel that I should also tell you about the scope of work that is undertaken in an average year to control outbreaks of the destructive pest species. During 1955, for example, approximately 2 million acres of coniferous forests in the western states were sprayed by aircraft to control the spruce budworm. Other large-scale projects also were undertaken to control the Engelmann spruce beetle in the Rocky Mountains, and the southern pine beetle in the southern states. In addition, there were many other projects conducted against bark beetles, defoliators, borers, sucking-insects, and others in almost all parts of the country.

Control projects in the United States vary tremendously in magnitude. While some of them are conducted at relatively small cost, others may require the expenditure of several millions of dollars before they are completed. They are, of course, conducted on lands of all ownership and they are financed either by the private land-owners alone; by county or state governments; or on a co-operative basis by the private owners, the states, and the federal government.

The control of forest insects has long been an integral part of the Nation's forest protection program. It has been intensified in recent years, however, in an effort to make it more commensurate in scope with the importance of damage and loss to the forests that insect pests cause. In view of the magnitude of the problem, as evidenced by the loss statistics contained in the Timber Resource Review, there is little question in my mind that it will be further intensified in the years to come. This will happen, in my opinion, because the owners and managers of forest lands are becoming increasingly aware of the losses that are caused by insects and they will not be willing to stand idly by and do nothing to prevent them.

No doubt I am stating an obvious fact when I say that a program in surveys to locate damaging populations of pest species will be needed throughout the country before control of forest insects can be made more effective. It is equally obvious, I suppose, that the extent to which it can be made more effective depends upon adequate coverage of the forested areas as a whole. It depends also, of course, on the extent to which outbreaks can be located in their early stages so that prompt measures can be undertaken to control them.

We have not always had an organized program in the United States to locate insect outbreaks in their early stages. Neither has there been concerted efforts in the past to watch over more than a portion of the total forested areas in the Nation for damaging infestations. There were, of course, many infestations that developed to epidemic size before anyone discovered them. The result, obviously, was severe tree-killing, excessive loss of valuable timber, and large expenditures for control after outbreaks had reached epidemic size. Several reasons can be cited why forest insect surveys were not more strongly emphasized in past years. I will not attempt to list all of them but I think I should mention the more important ones as a means of pointing up the changes that have occurred in survey work during the past decade. Until quite recently, there often was insufficient knowledge of how to suppress some of the outbreaks, particularly the tree defoliators, that occurred over extensive forest areas; the value of infested timber was not always sufficient to justify the cost of control even when effective methods were known; and, it was more or less a common belief a decade or two ago that an almost inexhaustible supply of timber existed throughout the Nation. The net result of these, and other reasons, was a general lack of concern about the toll of losses that insect pests caused to the forests of the Nation.

By the end of World War II, however, the entire concept about the need to protect the forests against insect pests changed. At about that time it was realized by almost everyone that timber supplies throughout the country were not inexhaustible. With the advent of DDT and aerial spraying, successful control of many destructive tree defoliators over large forested areas became a reality. The increased value of all timber species, even those that previously were considered not to be economical, prompted the use of control methods that previously were considered to be too costly. And finally, improved equipment and accessible roads for portable logging aided control in that they permitted the salvage of beetle-infested trees. Previously, most of these trees

were either inaccessible to logging, were destroyed during the process of control, or were left in the forest after control and not utilized.

In my opinion, however, the major event that fostered control of forest insects in the United States was enactment of the Forest Pest Control Act by the 80th Congress in 1947. My reason for believing so is that this Act established a basis for co-operation between the federal government, the states, and the private land-owners for financing pest control operations. Of equal importance, I believe, was that it provided for a federal program in surveys to detect and appraise infestations on lands of all owner-ships, and to determine whether there was need for measures to control them. It is under the provisions of this Act that the Forest Service, in close co-operation with the states and the private land-owners, now keeps as close watch as possible over most of the Nation's forests each year to locate insect outbreaks in their early stages. This practice thus permits the initiation of prompt measures for control wherever conditions are found that warrant control action.

I don't want to infer that there was no survey work of any kind done in the United States prior to the enactment of the Forest Pest Control Act. On the contrary, surveys of various kinds, and for various reasons, have been carried on for many years in all parts of the country. The work was done by many of the states, by the private land-owners and timber-operating companies, by the former Bureau of Entomology and Plant Quarantine of the U.S. Department of Agriculture, and by other agencies of the federal government. I believe I am correct by saying that most of the surveys that were conducted prior to the enactment of the Forest Pest Act, at least those by the Division of Forest Insect Investigations, were initiated to fulfill specific objectives in a broad program of work in forest insect research. Some of them, of course, were conducted in conjunction with specific projects that were undertaken for control.

I believe it would be to advantage to cite a few examples of these research-type surveys in order to point up the difference between them and detection and appraisal surveys which are now conducted by the Forest Service under the provisions of the Pest Control Act. Examples of the more common research-type surveys are as follows: (1) collecting and cataloguing the insect pests affecting specific hosts; (2) searching a forested area for the presence of an exotic pest; (3) determining the annual rate of tree-mortality caused by specific insects and relating the fluctuations in their populations to climatic, edaphic, or other factors; (4) determining the host preferences, and the relative importance of individual pest species in the forest complex; or (5) measuring and assessing the amount of tree-damage or tree-killing that resulted from an insect epidemic after the infestation had subsided. I won't take the time here to cite other examples of research surveys. I would like to mention, however, that some of them are still being conducted in most parts of the country and that they constitute an integral part of program work in forest insect research. They are being conducted not only by the Forest Service, but also by some of the states, a few of the colleges and universities, and even by a few of the major timber-operating companies.

Before I proceed to discuss detection and appraisal surveys that are conducted by the Forest Service, let me remind you again that they comprise a composite co-operative activity between the states, the private land-owners, and the federal government. I want also to emphasize that detection and appraisal surveys are not conducted as a separate entity in themselves as if divorced from the other work concerned with the control of forest insects. On the contrary, while the objectives, and some of the procedures, differ from research-surveys, they are closely related and together form an integral part of our forest insect research work. Furthermore, since research and surveys are both undertaken for the purpose of trying to reduce damage and loss that insect pests cause to the forests of the Nation, I feel that their close interrelationship is essential to the success of both program activities.

In the Forest Service, detection and appraisal surveys are a function of the Division of Forest Insect Research. At the Division's headquarters in Washington, D.C., they are co-ordinated by a Staff Assistant under the supervision of the Division Chief. In the field, they are conducted by technically trained entomologists at each of the nine Forest Experiment Stations in various portions of the country; at the



Forest Research Center, Juneau, Alaska; and at the Forest Insect Laboratory, Beltsville, Maryland.

It is at the Forest Experiment Stations that the responsibility lies for locating and keeping track of the status of insect infestations throughout the country. In meeting this responsibility, the Stations have developed, or are developing as rapidly as possible, a three-phase program. First, they are encouraging the voluntary reporting of information about the occurrence of insect outbreaks from co-operating personnel in other public agencies, from private land-owners, or from other individuals. Secondly, the Station entomologists conduct surveys on a planned basis to locate insect infestations in their early stages. Thirdly, and finally, they evaluate the entomological significance and the potential destructiveness of infestations that are reported, or those that they have detected, to determine whether control is needed, and if so, whether its undertaking would be biologically sound.

It is obvious, I think, that no single agency should be expected to assume the total responsibility for keeping track of the status and occurrence of damaging insect infestations throughout all of the extensive and diversified forests of the United States. The immensity of the task alone, I believe, is ample reason why detection and appraisal surveys are conducted on a co-operative basis. Another important reason, of course, is because of the mixed public and private ownership of the Nation's forests, a point which I mentioned earlier. In so far as possible, personnel who are co-operating with the Forest Service in the detection phases of the survey program are given training by the Station entomologists in the recognition of damaging insects and abnormal infestation conditions. They are also instructed in how and where to report their findings, and their reports are submitted by them entirely on a voluntary basis.

The detection surveys which are conducted on a planned basis to locate the occurrence of insect infestations in their early stages are undertaken by the Station entomologists to supplement the voluntary detection and reporting that is done by co-operators. These planned detection surveys have a two-fold objective: first, they supplement voluntary detection and reporting that is done by co-operators, and secondly, they assure, in so far as possible, that few or no serious infestations have escaped notice anywhere within the regions. Although the procedures that are used in the planned phases of detection surveys differ somewhat in the various sections of the country, there is considerable reliance on aerial observations to locate the occurrence of damaging insect populations.

Because of the large number of variables that must be taken into consideration when an evaluation is made of the entomological significance of an insect infestation, appraisal surveys are difficult to describe. There are few, if any, cut and dried methods that are always applicable for use in appraising any given infestation. For example, the species of insect, the age and vigor of the host, the status of knowledge of the effectiveness of parasites, predators, and diseases of the population, the degrees of stand susceptibility, vulnerability of adjacent or nearby timber stands to attack, climatic conditions, and many other factors must be taken into consideration in evaluating an infestation. Since all of the variables usually are in a state of flux, their effects on the population of the pest species also are variable. Regardless of the complexities that must be taken into account in evaluating damaging infestations, the entomologists strive to obtain uniform information from these appraisal surveys. In all cases they make as reliable an estimate as possible of the *extent*, the *intensity*, and the *trend* of each infestation that they examine. In addition, and of equal importance, they render the best judgment possible of (1) what likely will happen if no action is taken to suppress the infestation, and (2) what might be expected if prescribed methods are applied for control.

Let me tell you briefly the course of events that follow the evaluation of a damaging insect infestation before I describe the methods that are used for keeping track of their status and occurrence throughout the country. Results of the appraisal surveys are provided to the land-owner, the land-manager, or to Pest Control Action Committees in some regions, as promptly as possible. After considering the entomological and the economic aspects of the situation, the owner or manager then decides for or against the initiation of control. If control is decided upon, the entomologists usually

assist in the planning for the project so that it will be conducted in such a manner as to satisfy the entomological requirements for its successful completion. They often provide assistance in the technical aspects of the control undertaking, and, on occasion, even operate as technical project directors. After control has been applied, the entomologists again appraise the infestation and the land-owner or manager decides for or against its continuation.

I mentioned earlier that aerial observations are being used as much as possible as a means for locating the occurrence of damaging insect infestations. Aerial observations are proving especially useful for this purpose in most parts of the country, particularly in the West, and in many parts of the South, where the forests so often are comprised of large contiguous bodies of coniferous trees. They are useful also where the forests are either inaccessible from the ground, or where there is a lack of suitable vantage points to facilitate the early detection of important infestations from the ground.

It is fortunate, perhaps, that a majority of the major forest insect pests consist of tree-killing bark beetles and tree-defoliators, and that evidence of their occurrence in abnormal numbers usually is visible from the air. With few exceptions, coniferous trees that have been killed by bark beetles lose the green color of their foliage soon after they have been attacked. The occurrence of yellow or red-foliaged conifers in the forest, therefore, provides reliable evidence of an active bark beetle infestation. The tree species that show evidence of having been attacked and killed, and the way in which they are distributed in the stand, usually is indicative of the insect species that is involved. The relative abundance of the attacked trees, or the change in their number from one year to another, is a reliable indicator for the aerial observer to use in determining the status, scope, and intensity of an infestation, and its trend.

Aerial observations are useful in locating damaging infestations of defoliating insects because stands of defoliated trees also are quite visible from the air. Since these surveys are made to detect trees which have been defoliated by insect larvae, they are conducted most successfully during the first three or four weeks after larval feeding has been completed. An important requisite to the efficiency of aerial surveys for defoliators is the proper timing of observations. Therefore, aerial observations to locate defoliator infestations, and to delineate the scope and intensity of defoliation, must be done prior to the time when maximum evidence caused by larval feeding has been washed from the trees by rains, or blown from the trees by strong winds.

Suitable techniques for locating and mapping insect infestations from the air have been described by J. F. Wear and W. J. Buckhorn (1955) as follows: "The chief observer occupies the right front seat in the plane. He directs the pilot as to course to fly and determines the width of observational strip except when flight lines are predrawn on the map. At all times he determines the height to fly, closely follows the plane's course, and accurately draws the line of flight on the map as the flight progresses. He detects all types of insect damage, determines the tree species, and evaluates the damage. By knowing the exact position of the plane, he sketches in place on the map the type and intensity of the damage . . . When alone, the observer views the forested area on both sides of the plane. When there are two, the chief observer confines his attention to insect conditions forward and on the right side of the plane. The second observer, who occupies the left rear seat, detects and maps all infestations visible from the left side of the plane. If he lacks mapping experience he alerts the chief observer to map the infestation detected. Data mapped by the second observer are transferred to the chief observer's map upon completion of the day's flying".

In areas where there are insufficient land-marks to permit the observer to keep track of the position of the plane in flight, such as in the eastern portion of the Nation, course lines are drawn on a map in advance of the survey. These lines are then followed by the pilot with the aid of gyro compass bearings and the observers restrict their attention to infestations on a width of strip along each side of the plane. Records of observations usually are made by use of an electric operations recorder, an instrument which permits a correlation to be made between time and distance covered by the airplane, as compared with time and distance on the recorder chart. Thus, the observa-



tions that are made from the moving airplane are located and measured on the recorder chart and information is transferred to a map at a later time.

Several devices have been developed or adopted to aid the pilot and observers in the conduct of aerial survey operations. I will not take the time here to list and describe all of these aids. Suffice it to say that the airplanes are thoroughly equipped and properly maintained so as to insure the maximum safety for the crew. Special plexi-glass doors have been added to the planes to afford maximum lateral visibility; colored glasses or goggles which accentuate the difference in the color of foliage between damaged and undamaged trees usually are worn by the observers; strip-viewers, map-rolling devices, recording machines, and other aids also are used as the situation demands to improve the accuracy and effectiveness of the aerial survey operations.

In the event that I have over-emphasized the aerial phases of our surveys, let me explain that we are all fully cognizant of the limitations of the airplane in survey operations. We know only too well that not all damaging forest insect infestations can be observed from the air and we certainly do not advocate the replacement of all ground surveys by aerial methods. We recommend their use to the extent possible, however, because they are conducted at only a fraction of the cost that is required for similar coverage of the forested areas from the ground. In addition, the accuracy of information about the scope and trend of many infestations, particularly of bark beetles, usually is better when obtained from the air than when obtained from the ground.

Inasmuch as it is not always possible for aerial observers to identify the species of insect responsible for tree-killing, it usually is necessary to conduct ground surveys to complement, or to supplement, aerial observations. In our work, confirmatory ground surveys often are conducted by the aerial crews themselves, either on days which are unsuited for flying, or when the aerial observations have been completed. In addition to this, separate ground crews usually are needed at all of the Experiment Stations, not only to assist in this work, but also to assist in evaluating the entomological significance of most infestations that have been located.

In closing, I would like to mention that research is under way in most sections of the country to increase the accuracy and reduce the costs of our forest insect surveys. Various methods for locating infestations, and for evaluating their potential seriousness, are being explored. Aerial photography, using color transparency film, as well as panchromatic film-filter combinations, is being tested at various scales to determine its usefulness for appraising the scope and intensity of infestations. The accuracy of visual estimates and counts of infested trees on sample strips from the air are being compared to actual infestation conditions as determined from the ground. The number, size, shape, and distribution of sample plots that are needed for estimating accurately the scope and size of infestations is being studied; sequential plans for sampling insect populations are being developed; and the over-all accuracy and efficiency of our survey operations are being improved in many other ways.

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## DISCUSSION

F. P. KEEN. It would be of interest, perhaps, for Mr. Bongberg to state how many species of insects it has been possible to identify from the air in any one region.

J. W. BONGBERG. In the Pacific Northwest Region, an experienced aerial observer has learned to identify the tree damage and tree killing caused by 21 species of insects, bark beetles and tree defoliators combined.

W. L. SIPPELL. Would you please elaborate on how similar damage by two insect defoliators on the same host tree species is distinguished from the air?

J. W. BONGBERG. Knowledge of the life histories of the several tree defoliators is helpful in distinguishing between species affecting the same host tree. If more than one species occur on a single host at the same time, they cannot be distinguished.

A. E. BROWER. Is the balsam woolly aphid single brooded in the Northwest and why is late July the best time to detect the insect from the air?

J. W. BONGBERG. The insect is single brooded in the Northwest. Due to the altitude and the weather late July is the best time.

# Aim and Organization of the Forest Insect Survey in the Netherlands

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## ABSTRACT

*The Forest Insect Survey in the Netherlands aims to provide estimates of population density of forest insects of various species in successive years.*

*The authors describe several types of useful information drawn from the Survey records.*

*The organization includes 175 observers chosen from personnel of privately owned forests, state forests, municipal forests, institutions, etc. These observers are trained in making correct identifications. Details are given of the forms used by the survey and the methods of correlating the data.*

The aim of the forest insect survey in the Netherlands is to obtain estimates of the population density of the different pest species in succeeding years. This information is important for several reasons:

1) The data collected may be compared with those of previous years. Such a comparison shows, among other things which species are on the increase and which species have reached a dangerous level. The level is said to be dangerous, if severe damage is to be expected the following year, provided the increase in density continues at the same rate.

2) The data collected may be used for studying fluctuations in population density.

The following examples illustrate the above points. In 1950 it appeared from our observations, as well as from those supplied by special observers throughout the country, that the population of the common Pine Sawfly, the most noxious insect of our Scots pine stands, had reached a dangerous level. Some pine stands had already suffered severe damage. More severe infestations over large areas were to be expected in 1951. The forecast came true, and several thousand acres were totally or partially defoliated. It was the most severe outbreak ever recorded. Thanks to the data provided by the observers in 1950 the areas where the heaviest attacks might be expected in 1951 were known beforehand. Control measures could therefore be prepared before feeding began and stands threatened with defoliation were sprayed from the air before damage of any magnitude occurred.

Instances as mentioned under point 2 are the following: In 1955 a foreign entomologist, wishing to assess the importance of *Dasychira pudibunda* L. as a forest pest, requested a list of the outbreaks in the past years. The annual surveys enabled us to inform him that in 1947 and 1948 a few small beech stands in the central part of the country had been totally defoliated. *Dasychira pudibunda* L. is not a very harmful insect in our country as it feeds exclusively on beech and forests of that species only cover 2 per cent of the total forest area of the Netherlands.

At the Eighth International Congress of Entomology at Stockholm, Elton, a member of this Institute read a paper "*Dendroctonus micans* (Kugel), a pest of Sitka Spruce in the Netherlands". Most of the data on the years and location of infestations, as well as those on the tree species attacked, were taken from the annual survey information.

In the period 1940-45 Voûte made an enquiry into the causes of outbreaks of the European Pine Shoot Moth *Evetria buoliana* (Schiff.) and found a correlation between the severity of outbreaks over large areas and the rainfall in July. These investigations covered the years 1893-1945 and were possible because from 1940-1945 the degree of infestation was recorded in the annual surveys carried out by this Institute and from 1893-1940 in the Annual Reports of the State Forest Service and the Nederlandsche Heidemaatschappij.

These examples have shown that the existence of a forest survey organization is justified, even in a small country as the Netherlands with only 7 per cent of the area forested.

At the moment this survey organization includes about 175 observers. Fig. 1 shows how they are distributed over the country. The southwestern part of the



Fig. 1. The regions of the Netherlands showing the location of field observers and the percentage of each area under forest cover.

Netherlands and the two northern provinces are poor in forests; the observers in those parts are therefore more widely separated. It is clear that the total forest area should be covered. Forest ownership in the Netherlands is distributed as follows: privately owned forests 65 per cent; state forests 15 per cent; municipal forests 15 per cent; institutions etc. 5 per cent. The observers were chosen from the personnel of all the above mentioned groups so as to cover the total forest area as accurately as possible. Another important point is the correct identification of the insects causing damage.

In order to reduce the danger of misidentification as much as possible the observers receive a booklet giving in tabular form the most important characters of all except the most rare noxious forest insects, together with other information such as the time of the year in which the different stages occur, the food plants, the kind of damage done etc. We are confident that the common forest pests are rarely if ever misidentified. As to the rarer species the identification can usually be checked in various ways, such as visiting the infested stands or asking the observer to send a sample of infested material. The observers are urged to send specimens of insects or damage or both when in doubt.

The information required from observers is recorded on a simple form, which is distributed annually. The form contains four columns in which are recorded: the name of the insect concerned, the tree species attacked, the location of the affected stands, and the degree of infestation (light, moderate or heavy). When all forms have been returned the information contained is arranged in two ways. All data on the different insect species is extracted and treated under the names of the various species in tabular form. The information is also arranged according to the tree species attacked. For this purpose it is sufficient to tabulate the tree species and the different insects that attack each of them in parallel columns. Once the names of the insects attacking a certain tree are known all other information can easily be found under the insect names in the first tabulation.

The data thus arranged are published each year in the "Nederlandsch Bosbouw tijdschrift", a Dutch Forestry Journal and in a series of publications called "Mededelingen van het Itbon."

#### DISCUSSION

R. MARTINEAU. Who does the sampling in the field?

J. VAN DER DRIFT. Forest Rangers.

J. W. BONGBERG. Approximately how many reports are received annually from observers who find insect infestations in the country?

J. VAN DER DRIFT. May be seen in detail in the published annual reports.

W. J. CHAMBERLIN. What percentage of the country is in timber? Under what ownership is the timber? Is it on a short rotation and for what is it used?

J. VAN DER DRIFT. About 7 percent of the country is forested and the ownership is approximately as follows: State, 15 per cent; Municipal, 15 per cent; private, 65 per cent; and institutions, 5 per cent. The rotation is about 60 years, with a number of clearing crops. Pit poles are one of the most important products.





# Some Problems in Insect Surveys

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## ABSTRACT

The increasing number of state and regional lists, and of forest insect and other pest surveys, make a consideration of some of the basic factors involved desirable. An attempt is now being made both by federal and state agencies to forecast outbreaks. This is often based upon a single method of collecting, but insects are extremely diverse in habits and responses. Unrecognizable taxonomic differences, different physiological responses, cyclic influences, population pressures, migrations, weather conditions at particular periods, and other factors may greatly influence insect activity and consequently the results secured. Because of the foregoing, the methods being employed and the conclusions drawn may be open to question in many cases. This paper is a discussion of some of the factors involved in insect surveys.

More detailed knowledge of insect species, their subdivisions, their populations, and their past, present and probable future distribution is needed in many branches of entomology. State or other lists, regional and faunal studies, biological control projects and much of our taxonomy are based upon the assumption that we recognize the entities concerned, that we know their range, and that we have some idea of their numbers. How far from the truth the foregoing may be, merits examination. Our knowledge of these matters is so seriously lacking in many places that we may question the value of many statements made regarding insects, their distribution and their abundance. In spite of the obvious shortcomings in the data from surveys and other sources, quarantines and control projects must be based upon them.

American entomology may be said to have originated in northeastern America, but in that area we have as yet only two or three state lists of insects. Valuable as these are they leave much to be desired. Most of us have no state list of our insects to work with and no prospect of one. Most state and other lists are very incomplete in the species included, their distribution, time of flight, number of broods, and any definite indication regarding their relative numbers. Food plant records are full of inaccuracies in many lists. Because of their habits, some of the species, including some rarer ones (so far as numbers are concerned) are relatively easy to secure. Other species are not ordinarily taken by our collecting methods and are thought to be scarce or rare, when this may not be true at all. Knowledge of their habits, special collecting methods or work in the local areas which they inhabit will often yield such species in numbers. When we collect a species hitherto unrecorded from an area, the status assigned to it is so often mere guesswork; we do not know if it has previously escaped collectors, if it is an introduced species, if it is a species which has extended its range, or what its real category is.

The lack of records does not prove anything. Conspicuous day-flying widespread insects may elude the collector for his collecting lifetime. We have two butterfly collectors in Maine with more than twenty-five years experience, yet neither has seen the regal fritillary, *Argynnis idalia* Dru., only one of us has seen *Erora laeta* Edw. and *Glaucopsyche lygdamus* Dbldy. I have sought *Proserpinus flavofasciata* Wlk. all these years without seeing one, though it must occur throughout the state. The type of *Autographa surena* Grt. was taken in central Maine at Orono, about seventy-five years ago but I have not been able to learn of another record. It belongs in a group we expect to take readily at light and flowers. When we pass into the more obscure and less known moths, especially night fliers, the probability of securing them is small. When I took *Grapholitha libertina* Heinr. and *Griselda radicana* Wlshm. in Maine, these were known only from far western Canada, but certainly the former gives every indication of being a native. Both are related to important economic species and therefore are not species which would be disregarded. Other western and northern species have been discovered in Maine. On the other hand, collectors continue to discover in the Northeast colonies of species like *Nymphula broweri* Heinr. and *Crambus watsoni*

Klots which may be remnants of a fauna which flourished when the Continental Shelf along our eastern seaboard was dry land. Even in the case of species attracted by light or the usual baits, the percentage which is secured of a species flying in an area is doubtless small. The number is much smaller in the uncommon species; and in the case of the scarce and rare species the probability of securing a specimen is so small that we must term such a chance capture. The complex subject of bait and light attraction is in its infancy, though important work is being done. What then of species which are not attracted to light or bait, especially the smaller night flying species? We are too ignorant of large numbers of these to speculate. We know that some moths fly but a matter of minutes and when conditions are right. Many fly as a rule only in the immediate vicinity of their food plant or in their special habitat. The experience recounted by Henry Bird (1913) is enlightening. For many years his collecting light shone out over an area of salt marsh vegetation where *Apamaea erepta ryensis* Bird was breeding; yet he never got a specimen of this actively flying moth, until finally he discovered the larvae feeding there and reared them. The bulk of our insects belong to species which we have but a remote chance of securing by general collecting methods. We have scarcely begun to explore special habitats and microhabitats for their insects. My remarks have been based largely upon experience with the Lepidoptera, but apply even more forcibly to some of the other orders of insects. For insect surveys we have light traps, bait traps and other collecting devices. These secure for us a sample of the existing insect population. What do we know of that sample? We know that part of our species of Lepidoptera are not attracted to light and many species are not attracted to flowers or known baits. It would be foolhardy to say that such a device will secure the different species in proportion to the numbers existing in nature.

Extensions of the range of species, migration, mass movement or other influxes of large numbers of individuals are little understood. The conditions prompting movement, the directing principle, the effect of topography, winds, weather and other phenomena which may prompt or direct it, are all of great importance but little understood. The evident ease with which many species can move long distances in large numbers makes this a most important subject. There is accumulating evidence that many species well up and flow out in large numbers over large areas of country from which the species had been absent or nearly so. They may maintain a population for one or for a period of years before subsiding to what has been termed the natural or endemic range. The question whether or not the larch sawfly is a native or an introduced insect has been revived many times. We feel certain that the butterfly, *Plebeius saepiolus* Bdv., was not present in Scudder's day, but spread from the West and colonized Maine. It was discovered in Maine at Lincoln in 1929 and at Bar Harbor on the coast in 1933. The phalaenid moth, *Protagrotis niveivenosa* Grt., suddenly began appearing in catches in northern Maine about ten years ago, with no previous record. It increased to become in a few years a regular component of moth trap catches. We have no way of knowing whether or not this was the first invasion of northern Maine or if it is to be a permanent member of our fauna. Other less positive cases could be mentioned.

How do we determine when a species is endemic? In the case of many species any definite statement probably has little more value than to flatter our vanity. In the case of many of the less common species we have no way of evaluating their numbers. Then to cite the opposite extreme we might use the notorious spruce budworm. During the period about 1914 to 1919 large areas of timberland in Maine and elsewhere were stripped. The moths occurred in enormous numbers. Following this, in 1921 a forest entomologist was employed by Maine but not one definite record of spruce budworm reached his office for twenty years. Was the spruce budworm gone from Maine for a period of years? Did it in fact disappear from a large part of northeastern America? If it was still present (in an endemic state) was it restricted to a small portion of Maine? And what determined the territory it could occupy in this restricted endemic state? Then when there is a build up and the species passes out of the endemic state, what causes the change? It is easy to give the glib reply, "conditions are favorable"; but exactly what conditions were favorable; and how they counteracted the conditions which had maintained the endemic state is anyone's guess. An outbreak requires years to build up; therefore, not one or two favorable years but a series of favorable years

is necessary. What are these "favorable conditions"? Weather conditions vary greatly from year to year. Is the basic idea in this fallacious? Should we be looking for centers where a virile or dominant strain of the species arises and flows out in all favorable directions, hiding the endemic population under mass numbers? This continues until exhaustion of food in areas of maximum favorability and other inhibiting factors cause the species to drop again to an endemic state. Then what of this endemic population, if the foregoing occurred? Does the original endemic population persist through the vicissitudes of time (the migratory population disappearing), or does a real blend of the endemic and migratory strains occur, or is the small original endemic population swallowed up by the incoming masses and for all practical purposes eliminated? Too many of these questions await more information on population dynamics.

In spite of the foregoing inadequacies, quarantines and pest control projects are based upon the assumption that we have a workable understanding not only of the species, but also of the past, present, and probable future range of the pests and of their probable populations at different times. Many methods of securing the needed information concerning our insect pests have been tried. We have plots of many kinds; and these may be very valuable in the study of some species. In the case of forest-feeding species the use of plots is beset with many difficulties, such as the great areas concerned and difficulties of examination or checking. A basic difficulty is that insects see timberlands with different eyes than we do; consequently many sets of plots are unsatisfactory for the purpose desired, and many workers do not attempt to establish their plots until damage is evident in the area chosen, and this limits the data which can be secured. One of the difficulties is that the so-called natural conditions are not static. They are dynamic. One of the problems is to recognize when a plot has lost its value. Plot specifications are based upon the size, condition, growth and other factors related to the trees. But what do we find in plot specifications concerning the far more important consideration of the stage in the life and death struggle going on between the pest and its natural controls?

Entomologists are fully aware that the development of damaging outbreaks of most species and of many pest species is prevented as a rule by natural controls. Natural insect controls function without the assistance of man and without cost, and when the outbreak is permitted to take its course they are the factors which help bring control. Yet, these natural control factors are rarely evaluated when a spray project is planned. Once a spray program is put in operation it may be continued year after year in the belief that it will prevent damage, despite the fact that this may lead to outbreaks of other pests, favored by the spray used; or it may lead to the development of resistant strains of the pest. Michelbacher (1954) has pointed out that a spray application may not give control of the pest but nevertheless decimates the natural controls. These facts emphasize the need for a comprehensive survey both before and after application of a spray. The usual basis for determining a spray project is the amount of damage. Frequently the public demand for spraying stems from the amount of visible damage, which means that the spray will be applied after practically all the damage has occurred for that year or brood. Spraying offers the easiest and most publicized means of doing something to appease popular demand. It would be unfair to say that entomologists desire this state of affairs. The lack of adequate practical survey methods and the difficulties involved in getting basic data lead to this. We hear much about the importance of discovering centers of infestation of pests like the spruce budworm. The idea being that a spray can be applied to the limited center of infestation before food exhaustion initiates spread. There is abundant reason for saying that centers of biological control are far more important for the future of the forest; therefore, their recognition and protection is of much greater importance than a similar area where the pest dominates; but spraying these reduces them along with other areas of pest infestation. As Nature's controls bring an outbreak under control, man should have an opportunity to boost biological control agents and gain much additional help from them, but he seems nearly helpless in the face of this situation. Practical ways of determining when biological controls are reaching their climax surely can be developed, and some effort is being made in this direction in forest insects.

In orchards a determined attempt has been made by Pickett (1953) and his associates at the Fruit Insect Laboratory, Kentville, N.S. to evaluate the many biological factors and to reduce spraying to a minimum. How can we recognize pest outbreaks which nature is going to control and divert money which would be spent on worse than a fruitless project into more needed lines such as basic research? Can the entomologist develop ways to make big news of the victories won by his allies, the predators, parasites, etc. — bigger news than a spray operation? All of this leads to the conclusion that we must give more consideration to the basic inadequacies in our knowledge of insects and the effect this will have on surveys. We need to strive for much more knowledge: of the environment and the requirements of our insects; of insects as individuals, as species and as populations; and of insects as interacting components of a dynamic world.

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### DISCUSSION

W. A. REEKS. Dr. Brower mentioned the need for more life history studies of species captured by various techniques of sampling. To accomplish this end would it be more practicable to start the rearings from adults captured in live-traps or from field-collected larvae which are difficult to identify and often present in small numbers?

A. E. BROWER. Collecting gravid female moths offers a more direct and less expensive means of securing knowledge of the biology of many forest Lepidoptera than conventional survey methods.



# Der Forstschutzdienst gegen Insektenschädlinge in Bayern

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## ZUSAMMENFASSUNG

Das bayerische Waldgebiet umfasst  $2\frac{1}{4}$  Mill. ha.  $\frac{1}{3}$  davon sind Staatswald,  $\frac{2}{3}$  Kommunal- und Privatwald. Forstschutzmässig unterstehen letztere der Staatsaufsicht, die von 300 Forstämtern mit rund 2,300 geschulten Beamten ausgeübt wird. Grosse Teile des Waldgebietes sind künstlich begründete Monokulturen auf ungünstigen Standorten und durch Forstschädlinge besonders gefährdet. Hauptholzarten sind Fichte und Tanne mit 51%, Kiefer und Lärche mit 31%, Buche mit 9% und Eiche mit 5% der Waldfläche. Durch Grossschädlinge periodisch stark bedroht werden besonders Kiefer (*Panolis piniperda*, *Bupalus piniarius*) und Fichte (*Lymantria monacha*). Verschiedene Kulturschädlinge, sowie Gelegenheitsschädlinge sekundärer Natur erlangten in den Nachkriegsjahren Bedeutung.

Die Forstinsektenüberwachung des Gesamtgebietes wird vom Institut für angewandte Zoologie in München ausgeübt. Neben der Bearbeitung forstentomologischer Forschungsaufgaben und der Schulung der Forststudierenden betreut es den ganzen bayerischen Waldbesitz in einschlägigen Forstschutzfragen. Hauptaufgabe des Ueberwachungsdienstes ist die rechtzeitige Bekanntgabe drohender Massenvermehrungen von Gross- und Gelegenheitsschädlingen und die Ausarbeitung von Unterlagen zu ihrer Bekämpfung. Hierzu wird alljährlich im Winterhalbjahr auf Grund von "Probepuppensuchen" (unter Berücksichtigung der Parasitierung) im Gesamtgebiet die Populationsdichte der wichtigsten Grossschädlinge ermittelt. Erreicht oder übersteigt sie die "kritischen Werte", dann wird das bedrohte Gebiet kartenmässig erfasst und für Bekämpfungsaktion (mit insektiziden Nebeln) vorgesehen. Als "kritisch" gelten Populationsdichten, bei denen Kahl bzw. Todfrass auf Grossflächen zu erwarten ist. Zur Warnung der Praxis wird jeweils im Frühjahr eine "Forstschädlingsprognose" für das laufende Jahr veröffentlicht. Kultur- und Gelegenheitsschädlinge werden durch die örtlichen Dienststellen der Forstverwaltung bekämpft. Grossschädlinge unter Einsatz staatseigener Bekämpfungsgeräte durch einen besonderen technischen Dienst der Verwaltung.

Von den 9 Bundesländern Westdeutschlands, die zusammen eine Waldfläche von 6,8 Mill. ha aufweisen, ist Bayern mit einem Anteil von 2,3 Mill. ha das walddreichste. Ein Drittel seiner Waldfläche ist Staatsbesitz, zwei Drittel sind Kommunal- und Privatwald. Durch gesetzliche Regelung unterstehen auch diese forstschutzmässig der Staatsaufsicht, doch wird die praktische Durchführung notwendiger Forstschutzmassnahmen zuweilen erschwert infolge der starken Zersplitterung des Kleinprivatbesitzes, in Flächen, die oft nur wenige ha umfassen.

Im übrigen wird die Forstschutzaufsicht von 300 Staatsforstämtern ausgeübt. Sie sind über ganz Bayern verteilt und verfügen über einen Stab von rund 2300 Forstbeamten, die auch forstentomologisch geschult sind.

Auch waldbaulich zeigt Bayern unter allen Bundesländern grösste Mannigfaltigkeit. Sie wirkt sich auf die Schädling fauna seiner Wälder aus und ist bedingt durch erhebliche Unterschiede der Höhengliederung des Landes, sowie solche seines Klimas und seiner Bodenverhältnisse.

Seine Waldgebiete verteilen sich von rund 200 m Meereshöhe im Norden bis zu 1800 m, was der oberen Grenze der Baumregion im bayerischen Alpengebiet entspricht. Die langjährigen Niederschlagsmengen wechseln gebietsweise von 500 mm auf der einen Seite bis zu 1800 mm und darüber auf der anderen; die langjährigen Julitemperaturmittel von etwa  $14^{\circ}\text{C}$  bis zu  $18^{\circ}\text{C}$ . Der Waldboden variiert zwischen geringwertigen Böden des Buntsandsteins, tertiären Dünen sanden und diluvialen Schotterterrassen bis zu hochwertigen Moränen und Urgebirgsböden.

Forstschädling skatastrophen grossen Ausmasses sind in diesem Gebiet ziemlich streng gebunden an Höhenlagen unter 600—700 m, die nur ausnahmsweise überschrit-

ten werden, sowie an Gegenden und Jahre mit niederen Niederschlagsmengen und an geringwertige Böden. Besonders gefährdet sind in diesem Zusammenhang ausgedehnte Teile jener Forsten, die künstlich als Monokulturen auf ungünstigen Standorten begründet wurden.

Hauptholzart der bayerischen Wälder ist die Fichte (*Picea excelsa*), die zusammen mit der nur gering vertretenen Tanne (*Abies pectinata*) 51% des Waldbodens einnimmt. Sie dominiert in den grossen, mehr oder minder zusammenhängenden niederschlagsreichen Waldgebieten der bayerischen Alpen, in jenen des bayerisch-böhmischen Waldes entlang der tschechischen Grenze und im Frankenwald.

An zweiter Stelle steht die Kiefer (*Pinus silvestris*), die mit der anteilmässig nur schwach vertretenen Lärche (*Larix europaea*) 31% der Waldfläche besiedelt. Sie ist in den niederschlagsärmeren Gebieten Mittelfrankens, im alten Reichswaldgebiet um Nürnberg und in Teilen der Oberpfalz sowie Oberbayerns die herrschende Holzart.

Buche (*Fagus silvatica*) und Eiche (*Quercus sessiliflora* und *Q. pedunculata*) sind mit 9% bzw. 5% an der Waldfläche Bayerns beteiligt. Ihr Hauptgebiet liegt im nördlichen Bayern, in den grossen Wäldern des Spessarts und der Rhön.

Durch grossflächig auftretende Bestandsschädlinge stärker bedroht werden besonders Kiefer und Fichte. Die Tanne ist nur an der unteren Grenze (400 m) ihres natürlichen und innerhalb ihres künstlichen Verbreitungsgebietes gefährdet. Laubhölzer wie Buche und Eiche sind dank ihrer guten Wiederbegrünung vergleichsweise wenig bedroht.

Forstliche Hauptschädlinge sind in Bayern für Kiefer die in manchen Gegenden periodisch in Massenvermehrung tretende Kieferneule (*Panolis flammea* Schiff.) und der Kiefernspanner (*Bupalus piniarius* L.). Für die Fichte spielt die Nonne (*Lymantria monacha* L.) eine ähnliche Rolle. Die Tanne erfährt besonders im jugendlichen Alter in den angedeuteten Lagen oft fühlbare Ausfälle durch die bösartige Tannenlaus (*Dreyfusia nüsslini* C. B.). An Buche tritt in Nordbayern periodisch auf Grossflächen und bis zu Kahlfrass gesteigert der Buchenrotschwanz (*Dasychira pudibunda* L.) in Massenvermehrung, an Eiche in Unterfranken neuerdings der Eichenwickler (*Tortrix viridana* L.) in ähnlicher Weise.

An Dauerschädlingen sind nur wenige Arten und auch diese nur örtlich begrenzt vertreten: so etwa die Kleine Fichtenblattwespe (*Lygaeonematus abietum* Htg.) und die Fichtengespinstblattwespe (*Cephaleia abietis* L.) in Teilen des Frankenwaldes.

Gewisse Borkenkäferarten der Fichte und Tanne (*Ips typographus* L., *Pityogenes chalcographus* L., *Pityokteines curvidens* Germ.) sowie einige andere Sekundärschädlinge spielen dank sorgfältiger Ueberwachung in Bayern im allgemeinen nur die Rolle von Gelegenheitsschädlingen. Massenvermehrung und Grossschäden dieser Arten traten nach fast 80-jähriger Ruhe erstmals wieder nach dem Kriege auf und waren nachweislich durch besondere Verhältnisse der Kriegs- und Nachkriegszeit ausgelöst worden.

Unter den Kulturschädlingen an Fichte und Kiefer hat der braune Rüsselkäfer (*Hylobius abietis* L.) seit Einführung der neuen Kontaktgifte seine Rolle als Grossschädling ausgespielt.

Mehr örtliche, aber sehr nachdrückliche Bedeutung als Kulturschädlinge besonders für Kiefer besitzen die Engerlinge von *Melolontha* (*M. vulgaris* F. und *M. hippocastani* F.), gewisse Kieferntriebwickler (*Evetria buoliana* Schiff., *turionana* Hb. und *duplana* Hb.) sowie der Rindenwickler der Fichte (*Laspeyresia pactolana* Zll.). In den Laubholzgebieten Nordbayerns sind Buchen- und Eichenaufschlag sowie der Jungwuchs fast alljährlich durch Frostspannerfrass (*Cheimatobia brumata* L.) sowie verschiedene Kurzrüssler (*Strophosomus*- und *Phyllobius*-Arten) gefährdet.

Die Ueberwachung des Forstschädlingauftretens wird für ganz Bayern zentral durch das Institut für angewandte Zoologie der Forstlichen Forschungsanstalt München geleitet. Neben der Bearbeitung spezieller und in der Regel aktueller forstentomologischer Forschungsaufgaben, sowie der Prüfung neuer chemischer Insektenkampfstoffe und der forstentomologischen Schulung der Nachwuchskräfte für die höhere Forstbeamtenlaufbahn, berät und betreut es den gesamten bayerischen Staats-, Kommunal- und Privatwaldbesitz in allen Fragen des praktischen Schutzes gegen Forstschädlinge.

Mit der forstlichen Praxis steht es sowohl durch die Regierungs- und Staatsforstämter und deren Mitarbeiterstab als auch unmittelbar in Verbindung. In Bedarfsfällen werden durch die Mitarbeiter des Institutes örtliche Besichtigungen und Beratungen vorgenommen.

Zur Bewältigung seiner Aufgaben stehen dem Institut sechs planmässige Mitarbeiter (darunter drei akademisch geschulte Forstentomologen) und zur Zeit weitere fünf ausserplanmässige Kräfte zur Verfügung.

Hauptaufgabe der Forstinsektenüberwachung des Instituts ist der Forstschädlings-Warndienst durch langfristige Prognosen drohender Massenvermehrung forstlicher Grossschädlinge und die Ausarbeitung der Unterlagen zu ihrer Bekämpfung. Soweit Grosskampfkationen erforderlich sind, werden diese durch einen besonderen technischen Dienst der Forstverwaltung durchgeführt.

Grundlage der langfristigen Prognosen sind die Ermittlungen der Populationsdichte für die wichtigsten Grossschädlinge. Sie werden alljährlich vorgenommen und wurden in Bayern in den dreissiger Jahren zunächst für Kieferneule und Spanner eingeführt. Sie hatten sich im ganzen so gut bewährt, dass sie seitdem ständig weiterlaufen (von einer kurzen Unterbrechung während dreier Kriegs- und Nachkriegsjahre abgesehen).

Wir sind in Bayern dauernd bemüht, die Verfahren der Ermittlung von Populationsdichten für prognostische Zwecke zu vervollkommen und so auszubauen, dass nach Möglichkeit alle für das Land wesentlichen Forstschädlinge in die Prognosen einbezogen werden können. Bei einigen Arten, wie *Laspeyresia pactolana*, *Tortrix viridana* oder *Dreyfusia nüsslini* stösst die Ermittlung der Populationsdichte auf erhebliche Schwierigkeiten und ist gegenwärtig noch nicht befriedigend gelöst.

Langfristige Forstschädlingsprognosen müssen spätestens bis zu Beginn jeder Vegetationsperiode gestellt werden, damit die technischen Vorbereitungen etwa erforderlicher Bekämpfungsmassnahmen rechtzeitig eingeleitet werden können. Da die Vorarbeiten zur Ermittlung der Populationsdichte längere Zeiträume in Anspruch nehmen — besonders wenn es sich um Grosskalamitäten handelt — kommen für sie hauptsächlich jene Entwicklungsstufen der Forstinsekten in Frage, die im Herbst und Winter auftreten.

Soweit diese — wie die Puppen der Kieferneule und des Spanners und jene des Buchenrotschwanzes oder die Larven der Blattwespe — in der Bodendecke überwintern, oder wie die Engerlinge von *Melolontha* subterran leben, bereitet die Erfassung im Prinzip keine Schwierigkeit: Seitens der Forstämter, deren Waldbestände erfahrungsgemäss für die eine oder andere Art disponiert sind, werden nach den Anweisungen des Instituts im Spätjahr und Frühwinter (bei *Cephaleia* Ausgang des Winters) systematisch Probe-Bodenflächen abgesucht, die sich gleichmässig auf das Waldgebiet des Forstamtes verteilen.

Das gesamte in der Bodenstreu der Probefläche gefundene Insektenmaterial (ohne die Kleinfafauna wie Collembolen und Milben) wird dem Institut zur Auswertung übermittelt. Hier wird es nach Arten gesondert. Bei Forstschädlingen wird Gesundheitszustand und Parasitierungsgrad festgestellt, bei Eule und Spanner ferner Geschlechterverhältnis und weibliches Puppengewicht, bei Lydalarven der zu erwartende Schlüpf-Prozentsatz. Bei *Melolontha*-Engerlingen ist die Larvenzahl je qm und die Altersschichtung der Larven-Population von Bedeutung.

Die Ermittlung von Geschlechterverhältnis und weiblichen Puppengewicht ist nötig, da beides bei einigen Grossschädlingen jahrgangsweise erheblichen Schwankungen unterliegen kann. Beide Werte geben gewisse Anhaltspunkte über die künftige potentielle Nachkommenproduktion. Ihre Berücksichtigung für prognostische Zwecke ist daher wesentlich.

Die Zahl gesunder Individuen je qm wird nach Arten gesondert als Mass der Populationsdichte für jedes Forstamt bestandsweise registriert. (Für Eule und Spanner ferner Sexualindex und weibliches Puppengewicht.) Der Vergleich der Populationswerte mit jenen der Vorjahre ergibt Anhaltspunkte über Anstieg oder Absinken der Bevölkerung einer Art und über die Tendenz ihrer Bevölkerungsbewegungen.



Was die Grösse der Probeflächen anbetrifft, so liegt sie gewöhnlich zwischen 2—5 qm. Die Dichte des Probeflächennetzes ist je nach dem Gefährdungsgrad der untersuchten Waldgebiete verschieden. In harmloseren Fällen genügt nach unseren Erfahrungen das Absuchen einer Probefläche auf je 50—100 ha Wald; in ernsteren Fällen sollte auf mindestens je 10 ha Wald eine Probefläche entnommen werden.

In dieser Weise werden alljährlich in den bayerischen Kiefernwaldungen sowie in einigen seiner Buchen- und Fichtenreviere rund 20,000 qm Probeflächen abgesammelt und seitens des Institutes ausgewertet. In Krisenjahren — wie den verflossenen — erhöht sich Zahl und Umfang der Probeflächen auf 30,000 qm und darüber.

Schwieriger ist die Populationsdichte-Bestimmung bei der Nonne, die in Bayern den Hauptschädling an Fichte stellt. Sie überwintert bekanntlich im Stadium des Eies, das in kleineren Haufen unter Rindenschuppen versteckt abgelegt wird. Die Ueberseherfehler beim Absuchen der Stämme nach solchen Eihaufen sind gross und können bei ein- oder wenigen Gelegen je Stamm erfahrungsgemäss bis zu 100% betragen. Erschwerend kommt hinzu, dass die Nonne in normalen Jahren äusserst selten auftritt. Selbst in disponierten Beständen ist sie dann nur mit schätzungsweise 1 Falter und weniger je ha vertreten. Unter solchen Umständen ist ihre Populationsdichte auch nicht annähernd zuverlässig erfassbar.

Bei der Nonne beschränken wir uns daher darauf, Populationsdichte-Erhebungen nur in Fichtenbeständen und Jahrgängen durchzuführen, wo ihr Falterflug im Sommer bedrohlicher wird und auf jeden Stamm etwa ein Falter entfällt. Er ist vom Forstpersonal nicht zu übersehen. Hier werden von diesem Zeitpunkt an und in den folgenden Jahren, bis jede Gefahr beseitigt ist, eingehendere Ermittlungen durchgeführt.

Zunächst wird an Stichproben frischer Puppen noch im Sommer Gesundheitszustand, Geschlechterverhältnis und weibliches Puppengewicht festgestellt. Im Herbst werden systematisch auf das ganze bedrohte Waldgebiet verteilt an gefälltten Probestämmen die vorhandenen Puppenhülsen ausgezählt. Aus diesen Werten wird unter Berücksichtigung der bekannten Puppengewichts-Eizahlrelation die Zahl der Nonnen-eier je Stamm errechnet. Sie dient als Grundlage der Populationsdichte und der Prognose.

Was die Dichte des Probestammnetzes anbetrifft, so ist auch hier der jeweilige Gefährdungsgrad der Bestände massgebend. In Krisenjahren wird im Durchschnitt ein Stamm je 10 ha Waldfläche untersucht. In den Vorjahren einer Nonnenkalamität genügt ein Stamm auf je 20—30 ha.

Rein statistisch betrachtet ist weder das Verfahren des Probesammelns nach Bodeninsekten noch jenes der Puppenhülsensuche an Probestämmen einwandfrei. Die Ergebnisse der Populationsdichte schwanken von Probefläche zu Probefläche und von Probestamm zu Probestamm oft recht erheblich. Für statistisch zuverlässige Unterlagen müsste das Netz der Probeflächen und -Stämme, besonders in Zeiten geringer Gefährdung, wesentlich dichter gelegt werden.

Dies ist aus technischen Gründen nicht durchführbar. Es würde eine Vervielfachung des Mitarbeiterstabes des Instituts und eine zusätzliche Arbeitsbelastung der Forstämter bedeuten, der diese nicht mehr gewachsen sind.

Im übrigen zeigte die Erfahrung der verflossenen 25 Jahre, dass die langfristigen Forstschädlingsprognosen des Instituts, die auf dieser Basis fussen, in den meisten Fällen eintrafen.

Dies gilt besonders für die langfristigen Prognosen bei Kieferneule, Nonne und Buchenrotschwanz. Hier treffen die Voraussagen fast immer ein. Unzuverlässiger sind sie beim Kiefernspanner. Bei ihm versagen sie öfters. Es ist dies nach unserer Ansicht nicht auf statistische Fehler bei Ermittlung der Populationsdichte des Spanners zurückzuführen. Sonst müssten die Prognosen für Eule, Nonne und Rotschwanz, bei denen nach denselben Grundsätzen verfahren wird wie beim Spanner, ebenso häufig Fehlaussagen ergeben.

Das gelegentliche Versagen beim Spanner dürfte auf Mängeln beruhen, die jeder langfristigen Prognose anhaften, die auf lange Sicht mit dem Verlauf der Witterung und ihren Unregelmässigkeiten als einer unberechenbaren Grösse zu tun hat.

Im Vergleich zu Eule und Rotschwanz ist der Spanner während der Schwarm- und Eiablageperiode wesentlich witterungsempfindlicher.<sup>1</sup>

Die beiden ersteren sitzen in der Ruhe und bei ungünstiger Witterung mit ihren dachfirstartig ausgebreiteten Flügeln ziemlich fest und sind meist dicht der Stammrinde angeschmiegt. In dieser Lage bieten sie Wind und Regen geringe Angriffsflächen. Anders der Kiefernspanner: Er sitzt in der Ruhe locker, an den Nadeln der Kiefernkrone angehängt, mit tagfalterartig nach der Rückseite zurückgeschlagenen Flügeln.

In dieser Lage ist er den Einflüssen eines Unwetters wesentlich stärker ausgesetzt als Eule und Rotschwanz.

Dass es beim Spanner trotz hoher Populationsdichte zur Puppenzeit in der Folge häufig nur zu kaum bemerkbaren Frassschäden kommt, dürfte damit zusammenhängen. Dafür spricht, dass ein Ausbleiben solcher Frassschäden besonders nach Sommern festzustellen ist, wo während der Spannerschwarmzeit im Juni ungewöhnlich reiche Niederschläge herrschten.

So sind beispielsweise in diesem Jahr in einem Bestand des Spannergebietes bei einem Belag von 8 gesunden Puppen je qm im Mittel nur 159 Eier je Kiefernstamm abgelegt worden, statt der auf Grund der Prognoseunterlagen erwarteten 1,000 Eier. Auf Grund des Puppengewichtes war hier mit einer potentiellen Eizahl je Weibchen von 80 Stück zu rechnen. Im Mittel kamen aber nur 15—20 zur Ablage. Da während der diesjährigen Schwarmzeit gerade im Gebiet des Spanners wiederholt ungewöhnlich schwere, wolkenbruchartige Regengüsse niedergingen, ist die Störung seiner Eiablage sicher ihnen zuzuschreiben.

Was die Ueberwachung der Borkenkäfer anbetrifft, so wird sie im allgemeinen seitens der Forstämter selbst durchgeführt. Es kommt dabei alljährlich das bekannte Verfahren des Werfens von Kontrollfangbäumen zur Anwendung. Neben Anhaltspunkten über den jeweiligen Stand der Borkenkäferpopulation bietet es zugleich die Möglichkeit, Jahr für Jahr einen wesentlichen Teil der Nachkommenschaft des "eisenen Bestandes" abzuschöpfen. Nur in bedrohlichen Fällen wird hierbei das Institut in München beratend zugezogen.

Aehnliches gilt für verschiedene Gelegenheitsschädlinge, sowie für Kulturschädlinge wie *Hylobius*, *Melolontha*, *Laspeyresia pactolana*, Kieferntriebwickler usw.

Treten unvorhergesehen in der einen oder anderen Gegend neue Schädlingsarten in bedrohlichem Ausmass auf, so werden sämtliche Forstämter über die zuständigen Regierungsstellen durch Rundschreiben des Instituts verständigt und um Lagemeldung ersucht.

Das Ergebnis sämtlicher Unterlagen wird alljährlich zu Ausgang des Winters in einem ausführlichen Bericht der obersten bayerischen Forstbehörde vorgelegt. Er enthält Hinweise auf die in der bevorstehenden Vegetationsperiode drohenden Massenvermehrungen der wichtigsten bayerischen Forstschädlinge und Vorschläge nebst Unterlagen zu Gegenmassnahmen. Auszugsweise wird der Bericht in einer forstlichen Fachzeitschrift veröffentlicht und so auch zur Kenntnis der gesamten forstlichen Praxis gebracht.

Als Grundlage für die Bekämpfung der forstlichen Grossschädlinge gelten in Bayern die "kritischen Werte" ihrer Populationsdichte. Sie liefern bei Grosskampfaktionen zugleich das Material für die Ausarbeitung von Bekämpfungsarten, die vom Institut im Benehmen mit den Forstämtern an Hand der ermittelten Werte der Populationsdichten zusammengestellt werden.

Als "kritisch" werden dabei im allgemeinen jene Populationsdichten angesetzt, bei denen mit Kahl- bzw. Todfrass ganzer Bestände gerechnet werden muss.

Populationsdichten, bei denen nur leichte Frassschäden, wie Nasch- oder Lichtfrass, zu erwarten sind und die nur zu Zuwachsverlusten führen, werden im bayerischen Staatswald in der Regel noch nicht als bekämpfungswürdig behandelt. Es geschieht dies zum Teil aus wirtschaftlichen Gründen: die Kalamitäten brechen nach unseren Erfahrungen zuweilen zusammen, ohne ihre für den Wald tödliche Maximalentfaltung zu erreichen. Auch der Gedanke, die allgemeine Insektenfauna des Waldes nach Mög-

<sup>1</sup>Bei der Nonne, die im Eistadium in die Vegetationsperiode eintritt, spielt die Witterung in diesem Zusammenhang keine Rolle.



lichkeit zu schonen, spielt dabei mit. Angesichts der ausserordentlichen Breitenwirkung der modernen insektiziden Kampfstoffe wird sie bei Grosskampfkationen aufs härteste mitbetroffen. In besonderen Fällen werden Ausnahmen von dieser Regel gemacht: so etwa wenn ein Samenjahr der gefährdeten Holzart bevorsteht und aus waldbaulichen Gründen auf den Samenanfall nicht verzichtet werden kann.

Natürlich sind die "kritischen Werte" der Populationsdichte bei den einzelnen Grossschädlingen recht verschieden. Auch der allgemeine Zustand der bedrohten Bestände, ihr Alter, ihre Holzartenmischung, ihre Kronenbenadelung, die Wiederbe grünungsfähigkeit der bedrohten Holzart usw. sind zu berücksichtigen, wozu im Ernstfall jeweils eingehendere örtliche Studien nötig werden.

Als Richtlinie für die "kritischen Werte" der Populationsdichte gelten beispielsweise für Kieferneule und Buchenrotschwanz Grossflächenmittel von 3—4 gesunden

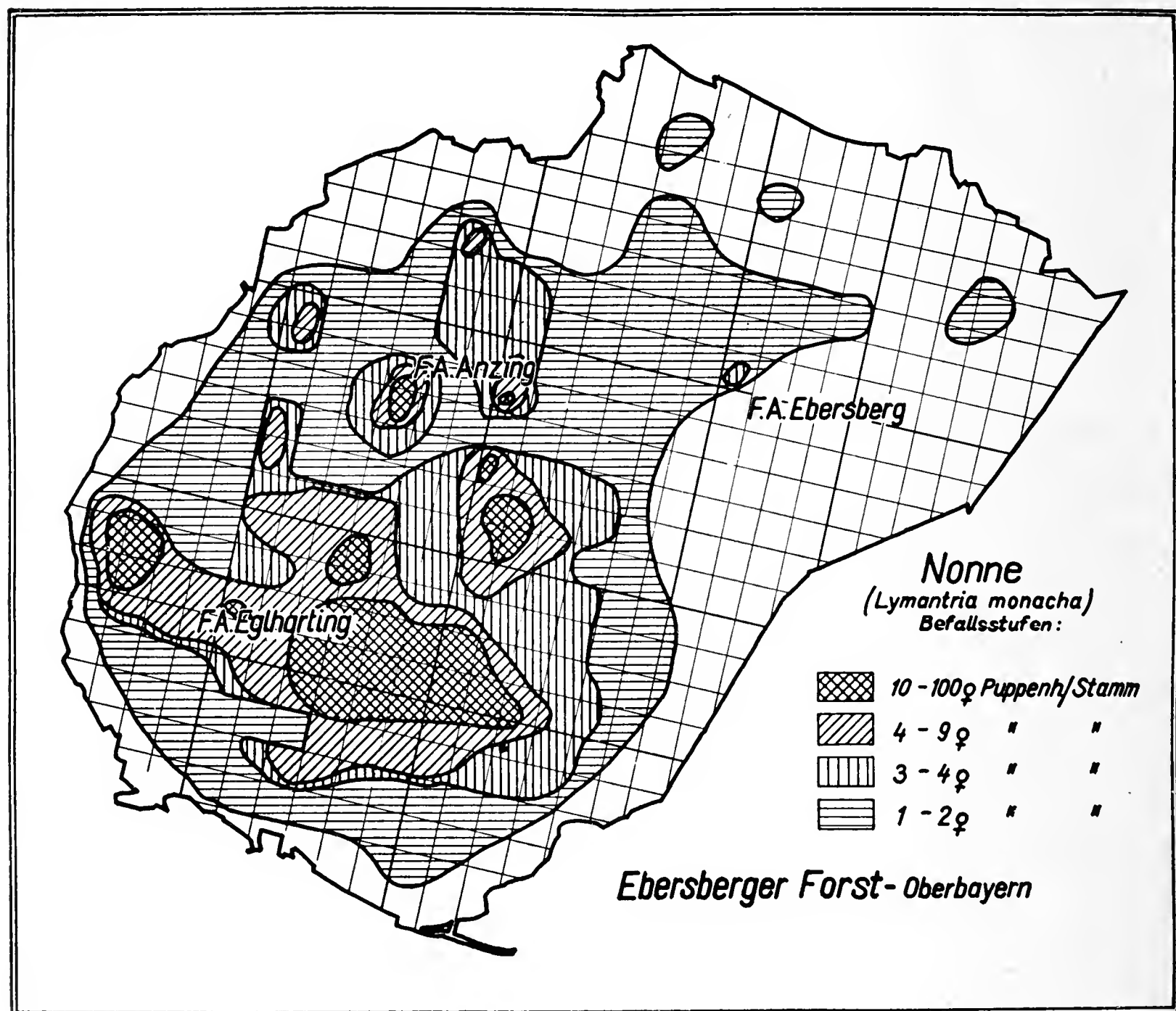


Abb. 1. Nonnenbekämpfung im Ebersberger Forst/Oberbayern 1955; Koordinatensystem und Suchpunkte.

Puppen je qm, für Kiefernspanner (unter den oben gemachten Einschränkungen) 15—16 Puppen je qm. Bei der Nonne setzen wir in Fichtenstangenhözern als gefährlichen kritischen Grenzwert je nach Alter des Holzes Eizahlen von 600—1000 je Stamm an. Für Fichtenalthölzer rechnen wir mit Nonneneizahlen von 1500 und darüber je Stamm als bedenkliche Werte. An Kiefer, an der die Nonne gelegentlich ebenfalls zu Massenvermehrungen schreitet, liegen die "kritischen Werte" ihrer Populationsdichte übrigens wesentlich höher wie an Fichte. Bei der Fichtenspinstblattwespe ist eine Schlüpfbereitschaft der Larven, die im Mittel zu 35 Wespen und mehr je qm führt, ein Zeichen für bevorstehende ernstere Frassschäden.

Die hier für einige Grossschädlinge genannten "kritischen Werte" der Populationsdichte sind rein empirisch in langjähriger Erfahrung in Bayern gewonnene Zahlen. Es scheint, dass man sie nicht ohne Vorbehalt für andere Gebiete übernehmen

kann. Wie sich im letzten Winter zeigte<sup>2</sup>, lagen beispielsweise die weiblichen Puppen- gewichte der Kieferneule bei ihrer derzeitigen Massenvermehrung in Holstein erheblich höher als im bayerischen Reichswaldgebiet um Nürnberg. Man wird daher die mitge- teilten "kritischen Werte" nicht ohne weiteres verallgemeinern dürfen.

Macht sich in einem mehr oder minder zusammenhängenden, ausgedehnten Wald- gebiet ein bedenklicher Anstieg der Populationsdichte von Grossschädlingen bemerkbar, der bis an ihre "kritischen Werte" heranreicht, dann werden schon im Herbst die Vorbereitungen für Bekämpfungsmassnahmen auf Grossflächen getroffen. Hierzu gehört die Ausarbeitung detaillierter Bekämpfungskarten in grossen Masstäben<sup>3</sup>, auf denen die gefährdeten und "bekämpfungswürdigen" Waldteile von den übrigen abgegrenzt sind.

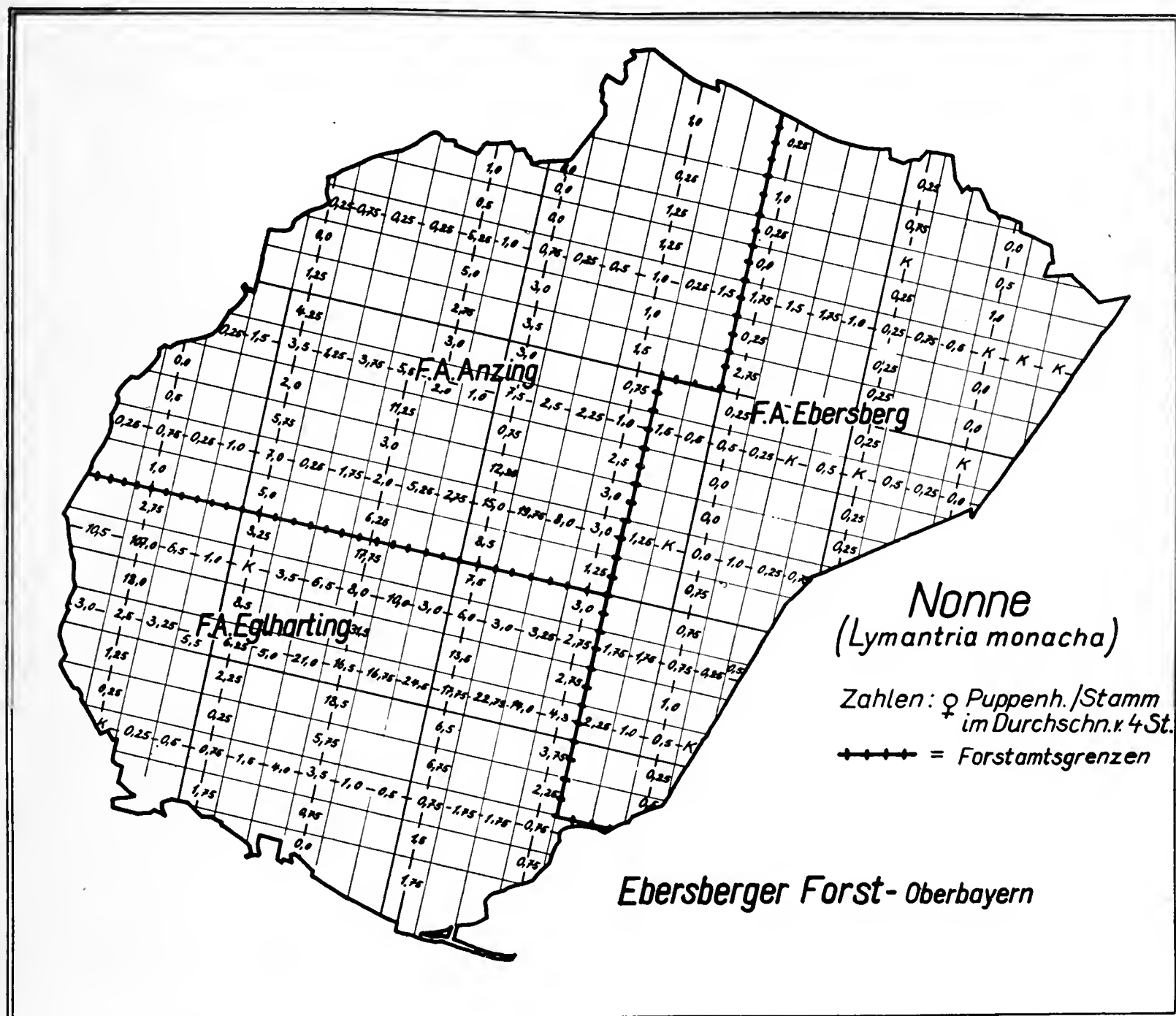


Abb. 2. Nonnenbekämpfung im Ebersberger Forst/Oberbayern 1955; Befallsgebiete nach Grös- senklasse I bis IV aufgeteilt.

Um die für die Bekämpfungskarten erforderlichen genauen Unterlagen zu erhalten, wird zunächst das Netz der Probeflächen bzw. Probestämme, die der Erfassung der Populationsdichten dienen, erheblich verdichtet und systematisch über das gesamte Waldgebiet verteilt. Bewährt hat sich hierbei ein Verfahren, bei dem ohne Rücksicht auf Verwaltungsgrenzen und Besitzverhältnisse die Stichproben entlang eines Systems von Längs- und Querkoordinaten vorgenommen werden, die 800—1200 m auseinander liegen.

Diese und die Suchpunkte werden in den Karten fixiert. Letztere liegen auf den Koordinaten, zweckmässig etwa 100 m auseinander.

Sowie das Untersuchungsergebnis für die einzelnen Suchpunkte vorliegt, wird die Populationsdichte unter Berücksichtigung ausschliesslich gesunder Individuen für den

<sup>2</sup>Ich verdanke diesen Hinweis einer freundlichen Mitteilung von Prof. Schwerdtfeger und Dr. Thalenhorst, Göttingen.

<sup>3</sup>Am besten bewährte sich der Massstab: 1: 10,000.

betreffenden Punkt in der Karte vermerkt. Liegen für alle Punkte die Ergebnisse vor, dann werden auf der Karte die bedrohten Waldteile, nach Gefährdungstufen (I. bis IV. Ordnung) gesondert, grossflächig zusammengefasst.

Derartige Karten dienen dem technischen Bekämpfungsdienst der Verwaltung als Unterlagen für die praktische Durchführung der Aktion.

Man kann gegen dieses Verfahren einwenden — und es ist von Seiten unseres technischen Dienstes auch geschehen — dass Bekämpfungskarten, die auf "langfristigen" Prognosen beruhen, unzuverlässig sind. Sie sollten sich besser auf "kurzfristige" gründen, die die Populationsdichten der Schädlinge in den Wochen unmittelbar vor der Aktion erfassen und den tatsächlichen Bestand besser wiedergeben.

Zweifellos sind kurzfristige Prognosen immer zuverlässiger als langfristige. Doch darf nicht übersehen werden, dass in grossen, oft 10,000 ha und darüber umfassenden Waldgebieten die Entnahme der Proben, ihre Untersuchung und Auswertung, sowie die Anfertigung der Bekämpfungskarten erhebliche Zeit beansprucht, die bei kurzfristigen Prognosen nicht zur Verfügung steht. Wir werden daher auch weiterhin an der langfristigen Prognose festhalten und ihre Nachteile wohl oder übel in Kauf nehmen müssen.

Die bekämpfungstechnisch günstigsten Entwicklungsstufen sind das 1. und 2. Raupenstadium — zum mindesten gilt dies für Lepidopteren, die für uns als Grossschädlinge in erster Linie in Betracht kommen. Diese Stadien sind vergleichsweise äusserst empfindlich und schon mit geringsten Dosierungen insektizider Kampfstoffe mit rund 100%iger Wirkung bekämpfbar. Bei Einsatz von DDT beispielsweise in Kiefernbeständen genügen hierzu 0,8 kg Wirkstoff je ha und weniger. Bei der ausserordentlich grossen insektiziden Breitenwirkung des DDT bedeutet diese niedere Dosierung zugleich eine gewisse Schonung der übrigen Insektenfauna des Waldes. Auch das 3. Raupenstadium ist noch relativ empfindlich, während die Altraupen erfahrungsgemäss etwas höhere Wirkstoff-Dosierungen erfordern.

Grundsätzlich wird daher in Bayern der Beginn der Aktion zu einem Zeitpunkt angesetzt, wo die Hauptmasse der Raupen im 1. und 2. Stadium steht. Dies ist der Fall, wenn rund 95% der vorhandenen (gesunden) Eier geschlüpft sind. Das Eischlüpfen wird deshalb vor Beginn der Kampagne durch die Mitarbeiter des Instituts im Kampfgebiet selbst überwacht. Unter Berücksichtigung der örtlichen Wetterlage lässt sich der entscheidende Zeitpunkt ziemlich zuverlässig 10—12 Tage voraussehen, was für die rechtzeitige Bereitstellung von Giftstoff, Geräten und technischen Personal wichtig ist.

Das Schwergewicht des Kampfes gegen die Jungraupen zu richten, bietet einen weiteren Vorteil: sie benötigen vergleichsweise die längste Entwicklungszeit. So stehen uns bei ihnen als günstiger Bekämpfungszeitraum rund 14 Tage zur Verfügung. Während desselben sollte bei normaler Wetterlage die Bekämpfung im wesentlichen durchgeführt sein. Bei Festsetzung der Geräte-Zahl, die einzusetzen ist, muss neben ihrer Tagesleistung und der Grösse des Kampfgebietes diese Bekämpfungsfrist zu Grunde gelegt werden.

Die praktische Durchführung von Grosskampfkationen ist Sache des technischen Bekämpfungsdienstes der Forstverwaltung. Er verfügt gegenwärtig über 5 Grossnebelgeräte (Tifa), die motorisiert sind und vom Boden aus eingesetzt werden, ebenso über das erforderliche, technisch geschulte Personal. Letzteres wird nur in Bedarfsfällen eingesetzt und ist für gewöhnlich im Rahmen anderer Forstverwaltungsaufgaben beschäftigt.

Von der Verwendung motorisierter Verstäubegeräte, die vor dem Kriege bei uns benutzt wurden, ist man inzwischen ganz abgekommen. Sie arbeiten im Forst nach unseren Erfahrungen wesentlich unwirtschaftlicher als die Nebelgeräte. Auch das Flugzeug wird aus ähnlichen Gründen nur ausnahmsweise eingesetzt: so wurden in diesem Jahr zwei Helicopter verwendet, die nach dem Sprühverfahren arbeiteten, da grosse Teile der gefährdeten Kiefernwälder auf anmoorigen Böden standen, die den Einsatz motorisierter Bodengeräte erschwerten hätten.

Nach allen, während des letzten Jahrzehnts in Bayern gemachten Erfahrungen, sind für Forstschädlingsbekämpfungen grossen Stils in zusammenhängenden, wegemäs-

sig gut erschlossenen Wäldern Nebelblaser (nach Art der grossen Tifa) die wirtschaftlichste Geräteform. Gegenüber den Stäube- und den Sprühverfahren gewährt der insektizide Nebel mit Tröpfchengrössen von 20—30  $\mu$  die feinste Verteilung des Giftstoffes und so mit geringster Dosierung höchsten Bekämpfungserfolg.

So ergab die Wirkungskontrolle bei den Grosskampfkaktionen der letzten beiden Jahre auf 8000 bzw. auf 5000 ha folgende Werte: In Kiefernwäldern wurde mit einer Durchschnittsdosierung von 0,8 kg DDT je ha (in 10%iger Lösung ausgebracht) eine Raupenabtötung von 99,9% erreicht. Aehnliche Wirkung bei gleicher Dosierung wurde im Vorjahr beim Spanner auf rund 500 ha erzielt. Gegen Nonne in Fichtenwäldern, die wesentlich dichter benadelt sind als Kiefernwälder, muss mit einer Dosierung von 1,0 kg DDT je ha gearbeitet werden. Bei dieser wurde im Vorjahr auf rund 5000 ha ebenfalls 99,9%ige Abtötung festgestellt.

Um wirtschaftlich zu arbeiten, setzt das Giftnebelverfahren zusammenhängende Waldflächen von mindestens 50 ha Grösse voraus. Auch soll es möglichst in geschlossenen Beständen eingesetzt werden. Für Kulturen ist es, der dort herrschenden komplizierten Thermik wegen, nicht geeignet.

Ein Nachteil des Verfahrens liegt in der starken Abhängigkeit der Giftnebelwolke von Luftbewegungen und der jeweiligen Thermik in den Beständen. Aus diesem Grunde ist tagsüber der Einsatz von Nebelgeräten im Walde völlig zwecklos. Brauchbare Arbeit leistet es in den frühesten Morgen- und späten Abendstunden. Die besten Ergebnisse erzielten wir bei Nachteinsätzen, wobei im Scheinwerferlicht gearbeitet wird.

Entscheidend für den Erfolg einer Aktion ist die sorgfältige Beachtung der Thermik im Walde, die grosse Anforderungen an den Geräteführer stellt und spezielle forstmeteorologische Erfahrungen erfordert.

Die Wirkungskontrolle bei Grosskampfkaktionen wird von geschulten Mitarbeitern des Instituts durchgeführt. Ihre Technik musste gegenüber den Vorkriegsverhältnissen vereinfacht werden: das früher benutzte Verfahren der Kotfallprüfung vor und nach der Aktion, wobei die Differenz des Kotfalls den Wirkungsgrad anzeigt, ist zu umständlich und zeitraubend, um bei Grosseinsätzen rechtzeitig ein örtliches Versagen und Ausbleiben des Bekämpfungserfolges erkennen zu lassen. Solche Feststellungen müssen kurzfristig getroffen werden im Hinblick auf etwa erforderliche "Nachbehandlungen".

Mit den modernen Kampfgeräten laufen aber Grossaktionen so rasch ab, dass eine Wirkungskontrolle, die auf Kotfall basiert, mit ihnen nicht Schritt halten kann. Auch verhindern die staubfeinen Kotballen der jüngsten Raupenstadien, gegen die jetzt das Schwergewicht des Kampfes gerichtet wird, zuverlässige Feststellungen des Kotfalles, die für Wirkungskontrollen erforderlich sind.

Die kurzfristige Wirkungskontrolle beschränkt sich jetzt daher auf stichprobenweise Stammfällungen (über Tüchern), verbunden mit Auszählung der überlebenden Raupen je Krone. Sie wird 2—3 Tage nach der Giftvernebelung eines Reviers durchgeführt. Ergeben sich dabei unter Berücksichtigung des Bestandesalters für die "Ueberlebenden" Zahlen, die für die laufende oder für die nächstjährige Vegetationsperiode noch stärkere Frassschäden befürchten lassen; dann wird der betreffende Revierteil nachbehandelt.

Die genaue Wirkungskontrolle wird abschliessend im Rahmen der alljährlichen Erfassung der Populationsdichte vorgenommen. Der Vergleich des Standes (gemessen an der Zahl gesunder Puppen je qm oder je Stamm) im Herbst des Bekämpfungsjahres zur Populationslage im vorausgehenden Herbst ergibt den endgültigen Wirkungsgrad, der bei der Aktion erzielt wurde. Bei seiner Ermittlung werden die Bevölkerungsbewegungen des betreffenden Schädlings in nichtbehandelten Beständen mit berücksichtigt.

Rund 24,000 ha Waldflächen wurden in den Nachkriegsjahren in Bayern im ganzen bei Grosskampfkaktionen mit DDT-Präparaten behandelt. Sie richteten sich gegen Nonne, Kieferneule, Kiefernspanner und Buchenrotschwanz. Von dieser Fläche sind 19,000 ha stets mit demselben günstigen Ergebnis nach dem Nebelverfahren bearbeitet worden.



Die chemische Waffe in der Forstschädlingsbekämpfung ist für uns nur ein Notbehelf. Im Interesse der Erhaltung einer artenreichen Insektenfauna unserer Wälder, die ihrem biologischen Gleichgewicht zugute kommt, wird sie im allgemeinen nur dann eingesetzt, wenn grössere Waldgebiete ernstlich durch einen Forstschädling bedroht sind. Im übrigen streben wir nach einem natürlichen Weg zur Eindämmung der Schädlingsgefahren und glauben, dass er in Massnahmen der Bodensanierung und des Waldbaues zu suchen ist. Ein Erfolg solcher "biologischer" Massnahmen ist aber der Natur der Sache nach nicht vor Jahrzehnten zu erreichen.



# The Canadian Forest Insect Survey<sup>1</sup>

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## ABSTRACT

*The Forest Biology Division of the Canadian Department of Agriculture conducts a nation-wide survey of forest insect conditions, making the information available to interested federal, provincial and industrial groups. The Forest Insect Survey was formally established in 1936 to fulfil a growing need for information and extension services. Its origin was closely related to the severe European spruce sawfly outbreak in Eastern Canada. During twenty years of operation there have been many changes in the Forest Insect Survey, particularly in the broadening of objectives, increased area coverage as new laboratories and facilities became available, and the establishment of a permanent field collection staff.*

*Currently, seven functional units of the Forest Insect Survey operate within prescribed regions of Canada. Geographic and local conditions make the further sub-division of two of these units necessary. Objectives and general methods are co-ordinated through Divisional Headquarters. The staff and facilities are reviewed in relation to a simplified description of the routine field and insectary operations of the Survey. The staff directly involved includes approximately 20 research officers, 20 technicians and 70 rangers. Over 20,000 insect collections are processed each year and much data are compiled in the form of infestation and damage maps. Survey information has been of considerable aid in numerous direct control operations.*

*In 1952, punch-card methods were adopted to record and analyse Survey collection data. The pertinent forms, methods, and codes are reviewed and explained. The utility of the system is considered, drawing examples from an annotated listing of forest Lepidoptera presently being compiled.*

*The Forest Insect Survey provides excellent opportunities, particularly since the acquisition of a field collection staff, for detailed biological and taxonomic studies as well as for more broadly based ecological problems.*

## INTRODUCTION

The great bulk of the forests of Canada are on Crown land and, as such belong to the Canadian people. As the major owners, the Provincial and Federal Governments are vitally interested in the protection of forest resources. Although the administration of forests has been vested largely with the provinces, the research and survey aspects of forest entomology have developed within a federal agency; the Forest Biology Division, Science Service, Department of Agriculture. The advantages of this arrangement are obvious, and need not be developed here. The significant feature is that it has led to the growth of a national, decentralized, but highly integrated group responsible for research and surveys of forest insects. Prior to 1936, all officers of the Division participated to a greater or lesser degree in both of these primary functions. The result was only limited survey information and frequent serious disruption of research activities. In 1936, the Forest Insect Survey was organized to assume the major responsibility for survey activities. The purpose of this paper is to review briefly the history of this organization, to set forth its present objectives, and, in a general way, to describe the methods employed, with particular emphasis on a punch-card system used for the recording and analysis of data.

## HISTORY OF THE FOREST INSECT SURVEY

Although the official history of the Canadian Forest Insect Survey only dates from 1936, in actuality its roots extend much farther back. On the appointment of Dr. J. M. Swaine as the first full-time forest entomologist in Canadian government service in 1912, Hewitt (1911) discussed the need for co-operative efforts with forest industries

<sup>1</sup>Contribution No. 368, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

in order to keep abreast of forest insect problems in Canada. In fact, a circular letter requesting information as well as insect specimens was sent out to the forest industries. Later, in 1928, at a time when serious outbreaks of the spruce budworm, larch sawfly, and bark beetles were extant in Canada, Dr. Swaine (1928) strongly recommended the establishment of an "intelligence service", to be conducted in co-operation with forest industries. A real attempt was made in 1931 to initiate the Forest Insect Intelligence Service. Special circulars on the principal forest insects were published, giving popular accounts of the life history and habits of the pests as well as coloured illustrations of the insects and their damage. These circulars, accompanied by questionnaires, were distributed to woods personnel with a request for reports on the occurrence of insects in their districts. The plan met with general approval and valuable information was received. The material results were limited, but they did facilitate the efforts a few years later of J. J. de Gryse, the late Chief of the Forest Biology Division. He had a firm belief in the necessity for a nation-wide survey organization and the serious European spruce sawfly outbreak in eastern Canada at that time afforded an excellent opportunity to launch a regional survey program designed specifically to follow the progress and spread of that insect. The generous support by representatives of forest industries through the agency of the Canadian Pulp and Paper Association and the Canadian Society of Forest Engineers should not go unrecognized.

In 1936, the regional survey in eastern Canada was started and 528 insect samples and records reached Ottawa for identification and recording. Encouraged by this start, de Gryse promptly proposed a national Forest Insect Survey to include forest insects generally. Other receiving centres were set up in 1937 at the existing Fredericton, N.B., and Vernon, B.C., laboratories. Similar activities were undertaken at laboratories at Indian Head, Sask., in 1940 and at Winnipeg, Man., in 1941. During these first years, the Forest Insect Survey was under the direction of Dr. A. W. A. Brown who remained in charge until 1942. The most pressing problems during that period were the development and maintenance of the co-operation of woods personnel as the major source of material and reports, and the means of handling and identifying the array of immature insects that began to flow to the receiving centres in ever-increasing numbers.

Before the war curtailed further development, two important trends in the Forest Insect Survey were forecast. To ease the problems of mailing and handling Survey collections, additional regional centres were necessary and demonstrated in the formation of Survey groups at Indian Head and Winnipeg. The second major development forecast was a ranger service of sub-professional staff to meet, instruct and encourage the co-operation of woods personnel. Both of these principles were pursued actively after the cessation of hostilities in 1945. Forest Insect Survey groups and eventually ranger staffs were established at Sault Ste. Marie, Ont., in 1945; Calgary, Alta., in 1948; and Victoria, B.C., in 1949. A sub-station under the Fredericton Laboratory was begun in 1949 in Nova Scotia at Halifax and later moved to permanent quarters at Truro. In 1953, the Sault Ste. Marie Laboratory accepted responsibility for all of Ontario and the original Ottawa Survey centre was disbanded. Recent territorial changes have involved the Prairie Provinces and Newfoundland. Survey activities at the Indian Head Laboratory, which had dealt with prairie shelterbelts, were discontinued in 1954 and the area of responsibility was sub-divided between the Winnipeg and Calgary laboratories. Following the construction of suitable facilities in Corner Brook, a Survey group undertook independent operations in Newfoundland in 1955. Previously, this Province had been given limited attention by the Fredericton Laboratory.

The present discussion would be incomplete without reference to Survey activities in the Province of Quebec. After participating in the programs for 1936 and 1937, the Quebec Government set up an independent Bureau of Entomology under the directorship of Dr. R. Gobeil. The vitally important European spruce sawfly problem in Quebec was an important factor in this decision. The Bureau has looked after survey activities in Quebec until the present time. From 1943 until 1952 Dr. L. Daviault was Director. Mr. R. Paquet is currently in charge.

The fact that Dr. A. W. A. Brown was in charge of the Forest Insect Survey from 1937 to 1942 has already been mentioned. During this period, a high degree of centralization was maintained. The absence of a successor to Dr. Brown and the

establishment of additional survey centres encouraged regional autonomy during the period that followed. Divisional conferences held in 1950 and 1951 dealt largely with Survey matters and led to the adoption of a national policy which included unified methods of recording data through the medium of punch cards. In 1952, the writer assumed the functions of Co-ordinator and transferred to Divisional Headquarters at Ottawa in 1953. Major developments during this recent period have concerned the inauguration of a punch-card system for recording and analysing data, re-organization and simplification of regional boundaries, clarification of the structure of the ranger service, and increased uniformity in basic procedures, methods, and forms, as well as broader appreciation of the scientific and technical potentialities of the Survey.

### OBJECTIVES OF THE FOREST INSECT SURVEY

After a rather rapid evolution during the first years of operation, the basic objectives of the Forest Insect Survey have changed little. Initially, the objective was only to follow the population level and spread of one insect, the European spruce sawfly. The enthusiasm of co-operators and the great diversity of insects received soon demonstrated the value of broadening the Survey to include forest insects generally. This concept was accepted and rapidly put into practice during the second and third years of operation. The co-operation of industrial and provincial groups continued to increase, and with these broadened horizons the full potentialities of the Survey began to be realized. These were expressed by J. J. de Gryse in 1951 when he said "From the economic standpoint, diagnosis and prognostication are the principal aims of the Forest Insect Survey. From the scientific angle, increased knowledge of certain phases of taxonomy, distribution, biology and cycles of abundance is the goal".

Although the general aims in the Forest Insect Survey have changed little, the methods and emphasis *have* undergone considerable adjustment. To explain these adjustments properly, it will be necessary to include more than a general reference to the Forest Biology Ranger service. This group constitutes the most distinctive feature of the Canadian Forest Insect Survey and has had a profound effect on its operations.

The primary purpose of the Forest Insect Survey has always been the detection of insect outbreaks and an annual census of forest insect conditions generally. Initially, field observations were accomplished almost entirely through the assistance of woods personnel of provincial governments and various industrial firms and associations. Contact was maintained through direct correspondence, widely distributed circulars, and occasional personal visits. The results obtained were encouraging but allowed only broad qualitative interpretation. The recognition of insect problems and the description of conditions by untrained persons was often disappointingly late and vague. From this emerged the concept of a ranger service consisting of a nucleus of trained non-technical men assigned to travel extensively in wooded areas meeting, instructing, and encouraging co-operators and also making collections and observations themselves. The results were not entirely as expected. Co-operator collections increased somewhat in number and value but were soon equalled or even overshadowed by the collections and observations made by the small ranger staff. As the number of rangers increased, reports of insect conditions became more comprehensive and complete. Research officers attached to the Survey became aware of the value and potentialities of selective controlled collections as a means of studying outbreaks and contributing to specialized research studies. It was this trend that led from what might be termed the "taxonomic phase" of the Survey to the present "ecological phase". It should not be inferred that the taxonomic problems of the Forest Insect Survey are by any means finished, but rather that the outlook has been enlarged to include studies beyond insect determination which remains as an important continuing problem. Most of the conspicuous forest insects, however, are fairly well known and recognized in all stages. There remains a vast assemblage of forest insects which, because of their sporadic appearance and limited economic importance, are relatively unknown. Until recently, the Survey was attempting to pursue a broad frontal attack on this entire assemblage. We are now convinced that better progress will result from a selective, group by group approach which may include taxonomic, morphological, life history, or ecological implications. This approach is dependent on being able to control to some degree the collections received at the

laboratory. This is feasible as Forest Biology Rangers now supply about 75 per cent of Survey collections. The general detection value of the remaining co-operator collections should not be discounted. Several thousands of persons are involved in submitting this fraction of the annual collection volume of nearly 30,000. The co-operation of provincial governments and woods industries by no means ends with submitting insect collections. Without their excellent field support in the form of such vital services as air and water transport, communication facilities, accommodation, and many others, the Survey could not hope to function in its present form.

In summary, the Survey began primarily and almost exclusively as a detection system, but with the acquisition of a year-round staff of rangers, the detection aspects have been improved and broadened and a sound research program is being developed. This transition has not been fully accomplished as yet, and has not been without some growing pains. One promising feature of the comprehensive program is that it allows the recruitment and retention of research officers who would find a routine detection organization a limited challenge.

To complete this section, I would like to summarize the current objectives of the Survey:

1. To collect, analyse, and publish as accurate and comprehensive information as possible on the status of all forest insects known to be capable of causing damage to Canadian forests. Attempts are being made to put this type of information on a quantitative basis through the use of various sampling techniques and procedures. In large-scale outbreaks, definite efforts are made to forecast the conditions for the coming season as an aid to agencies planning special control operations or cutting programs.

2. To establish the identity, in their various stages, of all insects which affect Canadian forests, and to ascertain the essential features of their biology, distribution, and natural control agents.

3. To contribute to the understanding of the general ecological interrelationships of the forest insect fauna and the forests of Canada through the accumulation of general Survey data supplemented by special observations and studies. These long-term

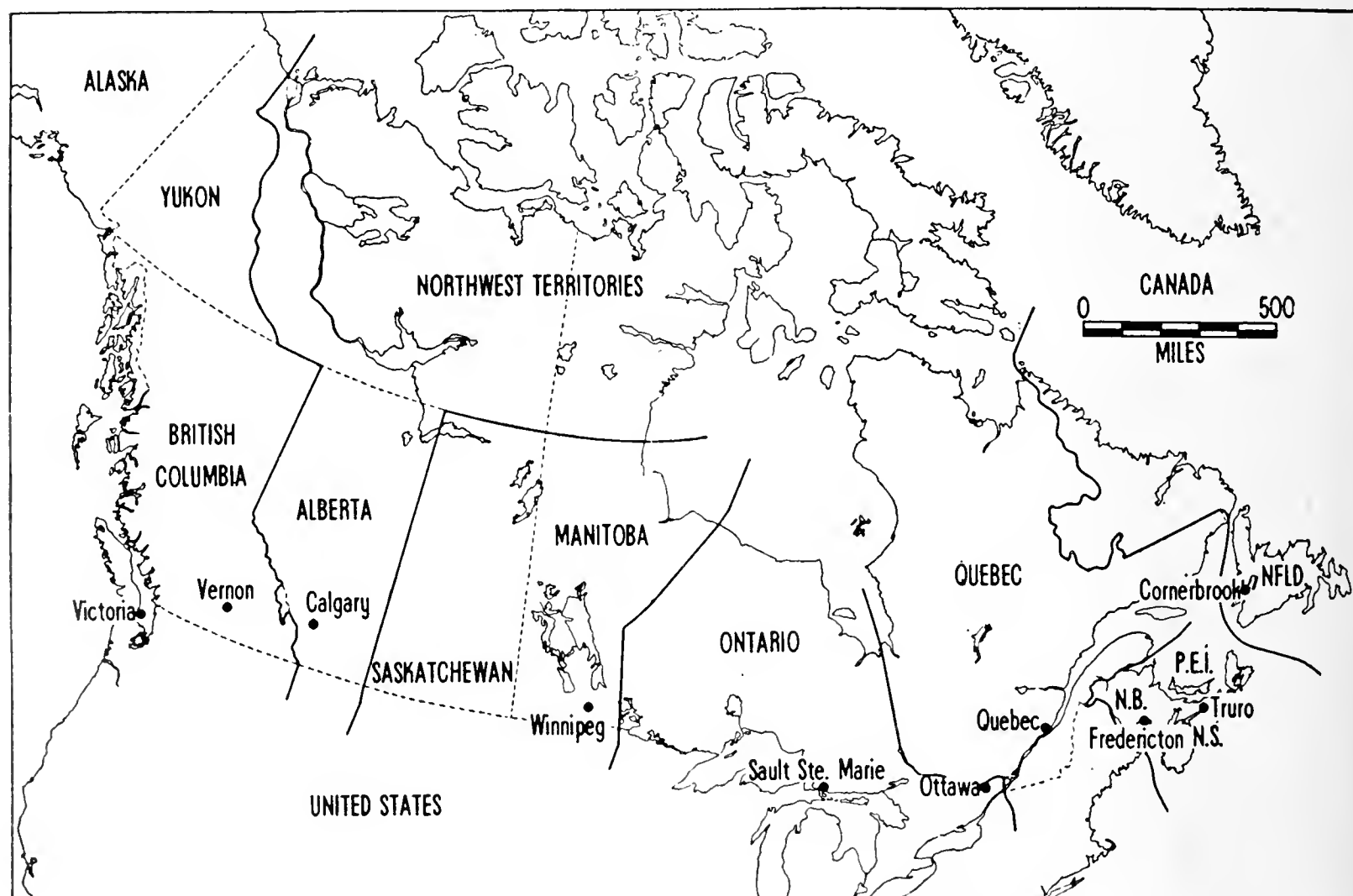


Fig. 1. A map of Canada showing the seven regions recognized by the Forest Biology Division and laboratories where Forest Insect Survey centres are located.



goals of the Survey include such topics as cycles of abundance and the association of certain insects with particular forest types and tree conditions.

The last two objectives are not ordinarily associated with a survey organization. In the Canadian Forest Insect Survey, these are largely a product of our unique ranger service. We also feel that the quality of work done in the pursuit of these objectives will ultimately, in a large measure, determine the value of the information secured and of the recommendations made as part of the first basic objective.

OPERATION OF THE FOREST INSECT SURVEY

The Forest Insect Survey, like the Forest Biology Division as a whole, is organized on a regional basis; there are seven major regions (Fig. 1) of which two are further sub-divided due to local circumstances. The regions with laboratory locations in parentheses are as follows: Newfoundland and Labrador (Corner Brook), Maritime Provinces (Fredericton and Debert), Quebec (Quebec), Ontario (Sault Ste. Marie), Manitoba and Saskatchewan (Winnipeg), Alberta and the accessible forested areas of the N.W.T. (Calgary), and British Columbia and Yukon (Victoria and Vernon). The Co-ordinator and one assistant are attached to Divisional Headquarters at Ottawa to unify, and standardize as far as practical, the objectives, points of emphasis, and basic procedures of the Survey. This group is also responsible for the integration of national reports and compilations.

Regional organization varies somewhat from location to location due primarily to local circumstances and the size of the staff involved. I would like to discuss a regional organization which embodies the main features typical of our laboratories (Fig. 2).

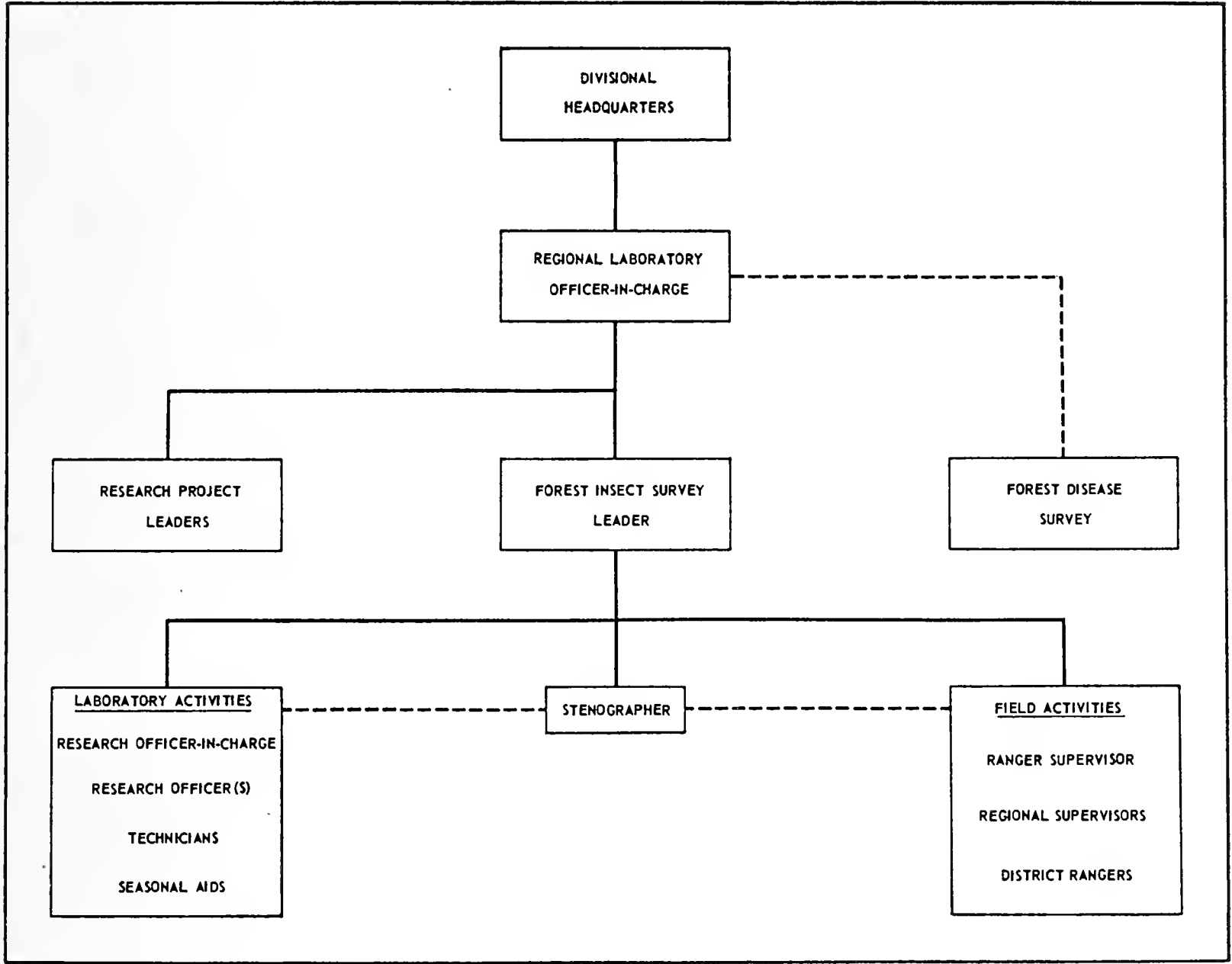


Fig. 2. A chart showing typical regional organization of the Forest Insect Survey and its relation to other regional functions.

The Forest Insect Survey forms one of the major projects of the laboratory and is under the general guidance of the officer-in-charge. The senior Survey officer has a sizeable and complex assignment requiring training in ecology and forestry as well as entomology.



One of his most important functions is to foster and maintain a high degree of liaison and integration between the field activities and the laboratory activities into which the Survey readily divides itself. In spite of the many organizational problems, we insist that senior survey officers maintain some personal research interest which may vary from specialized studies of some minor pest to a sampling problem or a broad ecological study.

The laboratory activities are under the direction of a research officer whose interests and training tend to be more basically entomological. He and his staff, which may include other research officers as well as technicians, are responsible for processing incoming collections, the rearing program, maintenance and development of reference collections, and the compilation and analysis of records.

Field activities of the Survey are under the immediate charge of a chief ranger. His major tasks involve supervision of the ranger staff, development and maintenance of field equipment, recruitment and training of ranger personnel, and, most important of all, participation in the general planning of the field programs of the Survey. To assist the chief ranger in his supervisory duties, the ranger staff is divided into sub-groups, each including a senior ranger or regional supervisor.

Each ranger is assigned for four or more field seasons to a specific territory. These ranger districts usually bear a close relationship to some administrative sub-division of the provincial forestry department. This arrangement greatly enhances and simplifies co-operative arrangements between the ranger and the provincial group most concerned with forest insect conditions. Districts vary greatly in size, forest type, insect problems, and ease of travel. Extremes may be found in the roadside and woodlot problems of heavily-populated southern Ontario with its network of roads, and the broad forested expanses of mountainous northern British Columbia where roads are almost non-existent.

With this general appreciation of the basic organization of the Survey, we can now trace the course of an individual collection from its origin in the field through the various laboratory operations that follow. A number of digressions from this main theme will be necessary to illustrate the maximum number of Survey features.

Forest Biology Rangers spend approximately six months in the field and the balance of the year at the regional laboratory where they fulfil a wide variety of important functions. Typically, field accommodation is provided for the ranger and his family by means of a house trailer or a cabin. Travel is largely by means of light truck-type vehicles. The abundance of lakes and waterways in many areas of Canada allow considerable travel by small boat or canoe. In areas with large bodies of water or extensive river systems, larger boats are used. Where provincial forestry departments maintain an air service considerable use is made of fixed-wing aircraft and helicopters.

By these various means a ranger travels extensively within his districts. His itinerary is governed by a fairly detailed work plan prepared before leaving his laboratory headquarters and by conditions he finds in the field. A variety of sampling methods are being used and tested. The classical method of beating trees over a mat is commonly used for defoliating insects at low to moderate population density. The most common shipping method employs a sturdy mailing tube approximately 5 inches high and 3 inches in diameter. Sufficient suitable foliage is included to serve as food and to prevent injury during shipment. Another common collecting technique is to remove sample branches with a pole clipper and net. Each collection is accompanied by the most valuable Survey document, the enclosure slip (Fig. 3). This form has been designed to yield the maximum amount of information considered feasible, in a format which is not only easy to complete but amenable to punch-card techniques. Enclosure slips are prepared in booklet form as duplicates so the Ranger may retain a copy. Items recorded on the enclosure slip are: date; collector and his mailing address; location by a variety of means including a national grid system; elevation; the tree described as to species, number, and average diameter; the type of collection; plot number if applicable; the general aspect or lay of the land; exposure of the trees; representativeness of the trees and the insect conditions thereon; and a description of the stand in terms of form, recent history, and cover type. Provision for remarks is also included. It should be noted that by completing the form, the Ranger has already assigned appropriate numeric code numbers to many of the variables. Collections are dispatched to a regional laboratory

**ENCLOSURE SLIP**

(All sections to be filled in by Forest Insect Rangers.  
Sections 7-12, optional for general co-operators.)

1. Date: Day 10 Month 7 Year 55

2. Collector F. B. Jones No. 09-216

Co. or Service \_\_\_\_\_

P.O. Address \_\_\_\_\_

3. Location of Collection Collection point #6 Libbey Pen.

Grid 6-091-228 County and Forest District Port Arthur 141

Section or Forest Division #24 Township Libbey Elevation \_\_\_\_\_

Range \_\_\_\_\_ Meridian \_\_\_\_\_

4. Tree Species Balsam fir 5. Type of Collection: 1. Beating  
No. Examined 4 (003) 3. Hand Picked  
Ave. D.B.H. 7" 5. Ground  
Perm. Sample Plot \_\_\_\_\_ 7. Bark or Wood  
\_\_\_\_\_ 9. Frass ( ) Q  
\_\_\_\_\_ 11. Traps

7. Aspect: 8. Exposure:  
1. Flat \_\_\_\_\_ 6. S. \_\_\_\_\_ 0. Unrecorded  
2. N. \_\_\_\_\_ 7. S.W. \_\_\_\_\_ 1. Shaded  
3. N.E. \_\_\_\_\_ 8. W. \_\_\_\_\_ 2. Partially Shaded  
4. E. \_\_\_\_\_ 9. N.W. \_\_\_\_\_ 3. Open  
5. S.E. \_\_\_\_\_ 0. Unrecorded \_\_\_\_\_ 4. Fringe

9. Were trees sampled representative of that species in the general stand?  
1. N.A. \_\_\_\_\_ 2. S. & I. \_\_\_\_\_ 3. S. \_\_\_\_\_ 4. I. \_\_\_\_\_

10. Stand Form: 11. Stand History (recent):  
1. Overmature \_\_\_\_\_ 1. Undisturbed \_\_\_\_\_  
2. Overmature (2-storied) \_\_\_\_\_ 2. Clear Cut \_\_\_\_\_  
3. Mature \_\_\_\_\_ 3. Selective Cut \_\_\_\_\_  
4. Mature (2-storied) \_\_\_\_\_ 4. Burn \_\_\_\_\_  
5. Immature (pole) \_\_\_\_\_ 5. Insect Killed \_\_\_\_\_  
6. Reproduction \_\_\_\_\_ 6. Windthrown \_\_\_\_\_  
7. Plantation \_\_\_\_\_ 7. Flooded \_\_\_\_\_  
8. Woodlot \_\_\_\_\_ 8. Grazed \_\_\_\_\_  
9. Old Field \_\_\_\_\_ 9. Doubtful \_\_\_\_\_  
10. Shade Tree \_\_\_\_\_  
11. Nursery \_\_\_\_\_  
12. Doubtful \_\_\_\_\_

12. Cover Type Bf. Sw.

13. Remarks Collection #2 from point #6.  
Larvae common; mostly in VI water.  
Four tracheas taken from each tree.

June 13/55      S55-3069

01 - *Choristoneura fumiferana*      78 larvae  
6-54-08-01

Fig. 3. Forest Insect Survey enclosure slip. Upper view shows face side as completed by a Forest Biology Ranger. Lower view shows reverse side as completed at the laboratory.

by means of first-class mail or railway express, and reach the laboratory within a few days except from particularly remote areas.

Collections are processed as promptly as possible after they reach the laboratory; usually within 24 hours. The mailing tubes are opened by an experienced technician and the contents carefully examined. The insects are identified as completely as possible

and those designated for rearing are placed in suitable containers; the remainder are discarded. A variety of aids such as empirical keys, charts, inflated or preserved larvae, are employed to assist in the identification of incoming material. Colour transparencies are also used. All these aids help to increase the number of species we are able to recognize. An assistant adds the appropriate information to the reverse side of the enclosure slip as illustrated in Fig. 3. The information includes the date of handling, the record number, and the insects involved by number and stage. The assistant also prepares any necessary rearing sheets and carries out a number of important coding functions as appropriate code numbers are required for variables not already coded automatically by completing the enclosure slip. These variables are: location, tree species, and insect species.

Within each region a location code has been developed to suit local requirements. It is usually based on Ranger districts and is a great convenience when compiling information for local use. The code is a simple two- or three-digit code and is shown in Fig. 3 as the encircled figures 141 which refer to Division 24 of the Port Arthur forest district.

Tree species are coded according to a national system using a modified block-type code (Fig. 4). The first digit allows for a rapid division of collections into coniferous,

HOST TREE CODE		
MISCELLANEOUS		
999	No host plant involved	
800	Miscellaneous trees, shrubs, herbs, etc.	
CONIFEROUS TREES		
001	<i>Abies</i> spp.	Fir
002	<i>amabilis</i> (Doug.) Forb.	Fir, Amabilis
003	<i>balsamea</i> (L.) Mill.	Fir, Balsam
004	<i>balsamea</i> (L.) Mill. var. <i>phanerolepis</i> Fern.	Fir, Bracted Balsam
005	<i>concolor</i> A. & G.	Fir, Silver
006	<i>grandis</i> (Dougl.) Lindl.	Fir, Grand
007	<i>lasiocarpa</i> (Hook.) Nutt.	Fir, Alpine
010	<i>Auracaria</i> spp.	Monkey Tree
011	<i>Cedrus</i> spp.	Cedar
012	<i>libani</i> Loud.	Cedar, Lebanon
013	<i>Chamaecyparis</i> spp.	Cedar
014	<i>nootkatensis</i> (D. Don) Spach	Cedar, Yellow
NON-CONIFEROUS TREES		
100	<i>Acer</i> spp.	Maple
101	<i>circinatum</i> Pursh	Maple, Vine
102	<i>glabrum</i> Terr.	
"	var. <i>Douglasii</i> (Hook.) Dipp.	Maple, Douglas
"	"                                  "	"                  "
"	"                                  "	"                  "
113	<i>specatum</i> Lam.	Maple, Mountain
120	<i>Aesculus</i> spp.	Buckeye
121	<i>carnea</i> Hayne	Horse-Chestnut, Red
122	<i>Hippocastanum</i> L.	Horse-Chestnut

Fig. 4. Excerpts from the Forest Insect Survey host tree code.

non-coniferous, and miscellaneous groups. The second and third digits are assigned so as to allow the easy separation of generic groups as for example firs, spruces, maples,

poplars, etc. The code provides for 255 species; 54 coniferous and 201 non-coniferous. The encircled figures 003 in Fig. 3 refer to balsam fir.

The coding of insect species was a much more involved problem and required a great deal of preparation. Regional lists were prepared of insects included in Survey files and integrated into one composite listing. This was carefully checked by taxonomic specialists of the Insect Systematics and Biological Control Unit before code numbers were applied according to a group-classification system. The following excerpt is a section of the Lepidoptera code.

6-54-00-00	Tortricidae
6-54-05-00	Argyrotaenia
-- -01	citrana Fern.
-- -02	juglandana Fern.
-- -03	lutosana Clem.
-- -04	mariana Fern.
-- -05	occultana Free.
-- -06	pinatubana Kft.
-- -07	quadrifasciana Fern.
-- -08	quercifoliana Fitch.
-- -09	tabulana Free.
-- -10	velutinana Wlk.
-- -11	alisellana Rob.
6-54-06-00	Argyrotoxa
-- -01	albicomana Clem.
-- -02	curvalana Kft.
-- -03	semipurpurana Kft.
6-54-07-00	Batodes
-- -01	angustiorana Haw.
6-54-08-00	Choristoneura
-- -01	fumiferana Clem.
-- -02	pinus Free.
6-54-09-00	Coelostathma
-- -01	discopunctana Clem.

The first digit "6" applies to all Lepidoptera. The Tortricidae is the 54th family of the Order according to the original alphabetical listing. Within the family, the genera are likewise numbered according to an alphabetical listing. The insect referred to in Fig. 3, the spruce budworm, *Choristoneura fumiferana*, has a code number 6-54-08-01. The code contains approximately 6000 species.


The registry of incoming samples has now been completed. Collections have been opened, numbered, identified as far as possible, allocated to rearing along with appropriate rearing sheets, and several complex variables have been coded. Three separate avenues remain to be followed; the acknowledgment procedure, the rearing program, and the transfer of data to punch cards.

Each collection received is acknowledged by mail to inform co-operators and to maintain contact with rangers. A standard form (Fig. 5) and window envelope are used. The collection number, the scientific and common name of the insects, and the number and stages received, are shown on the form. Every effort is made to acknowledge collections promptly.

Insect material designated for rearing is handled in a variety of ways, and under a variety of conditions. Only a brief generalized review is possible. At some laboratories, rearing is carried out in insectaries while at others, controlled rearing rooms are available. By following a planned, selective program, it is possible to maintain a reasonable balance between material handled and the available staff, which consists of one or more technicians aided by a staff of seasonal assistants. Records are kept on special rearing sheets which are relatively simple to use, and allow for keeping rather specific information, particularly on parasites. Insects which arrive at the laboratory dead, or that die soon after arrival, are diagnosed for the presence of disease organisms by specially trained technicians. Much of the adult material from the rearing program

SA 285  
19152-IPM-724

FOREST BIOLOGY DIVISION



CANADA

SCIENCE SERVICE

DEPARTMENT OF AGRICULTURE

F.B. Jones,  
Forest Biology Ranger,  
c/o Department of Lands and Forests,  
Port Arthur, Ontario.

Sault Ste. Marie, Ontario.  
June 14, 1955.

Dear Sir:

We wish to acknowledge receipt of the following collections:

Rec. No.	Food Plant	Names of Insects	Status
955-3047-01 (215)	Pin Cherry	Malacosoma pluviale - 50 larvae	
955-3069-01 (216)	Balsam fir	Choristoneura fumiferana - 78 larvae	
955-3075-01 (217)	Wt. Spruce	Choristoneura fumiferana - 12 larvae	
-02		Dioryctria reniculella - 3 larvae	

STATUS OF FOREST INSECTS

A. Forest insects known to be causing serious damage at the present time.

B. Forest insects not causing serious damage at the present time, but known to be capable of doing so.

C. Forest insects which have never been known to cause serious damage.

D. Forest insects about which we know very little. We should like to get more of these.

E. Useful or beneficial insects.

Your co-operation with the Forest Insect Survey is of great value, and is much appreciated.

Yours very truly,

Officer-in-Charge of Survey.

Fig. 5. Forest Insect Survey acknowledgment form.

is pinned and labelled for final confirmation of identification by the Insect Systematics and Biological Control Unit at Ottawa. The assistance of these specialists is valuable in lending continuity to our nomenclature and in our attempts to increase our knowledge of Canadian forest insects. Over-wintering stages of insects are kept in cold rooms and incubated in the early spring in advance of the field season.

The recording of Survey data on punch cards has already been noted in descriptions of the enclosure slips and opening procedures. In review, information on 12 variables is recorded on a special enclosure slip (Fig. 3) which accompanies each collection. This process automatically codes most of the variables. Three complex variables dealing



[illegible]

been designed to simplify the punching procedure as far as possible. All information from the reverse side of the enclosure slip (Survey number, insect, stages, etc.), is entered in the first 23 columns of the upper bank of the card. The lower bank, from columns 45 to 84, contains the variables appearing on the face side of the enclosure slip and in the same sequence. If the insect material is reared at the laboratory, there is provision for recording in code the occurrence of diseases and parasites as well as the source of the insect determination (columns 85-90). The remaining space in the upper bank provides for listing any parasite species recovered. Parasite information in this form is only of reference value, and for machine analysis must be recorded on separate "parasite cards" (Fig. 7), one card for each species. All the data from the "host card" is duplicated on each parasite card and the parasite identity is added in code in columns 24 to 30. Host cards are used for most compilations and analyses, but when the interest is in parasites, the parasite cards are available for study, and allow ready reference to all features of the original collection.

In concluding this section, a few words would be in order on the various means by which Forest Insect Survey information is made available to interested parties. During the field season each main laboratory circulates within its region at monthly or regular intervals a brief summary of insect conditions. When more prompt and general dissemination of information is warranted, newspaper and radio facilities are used.

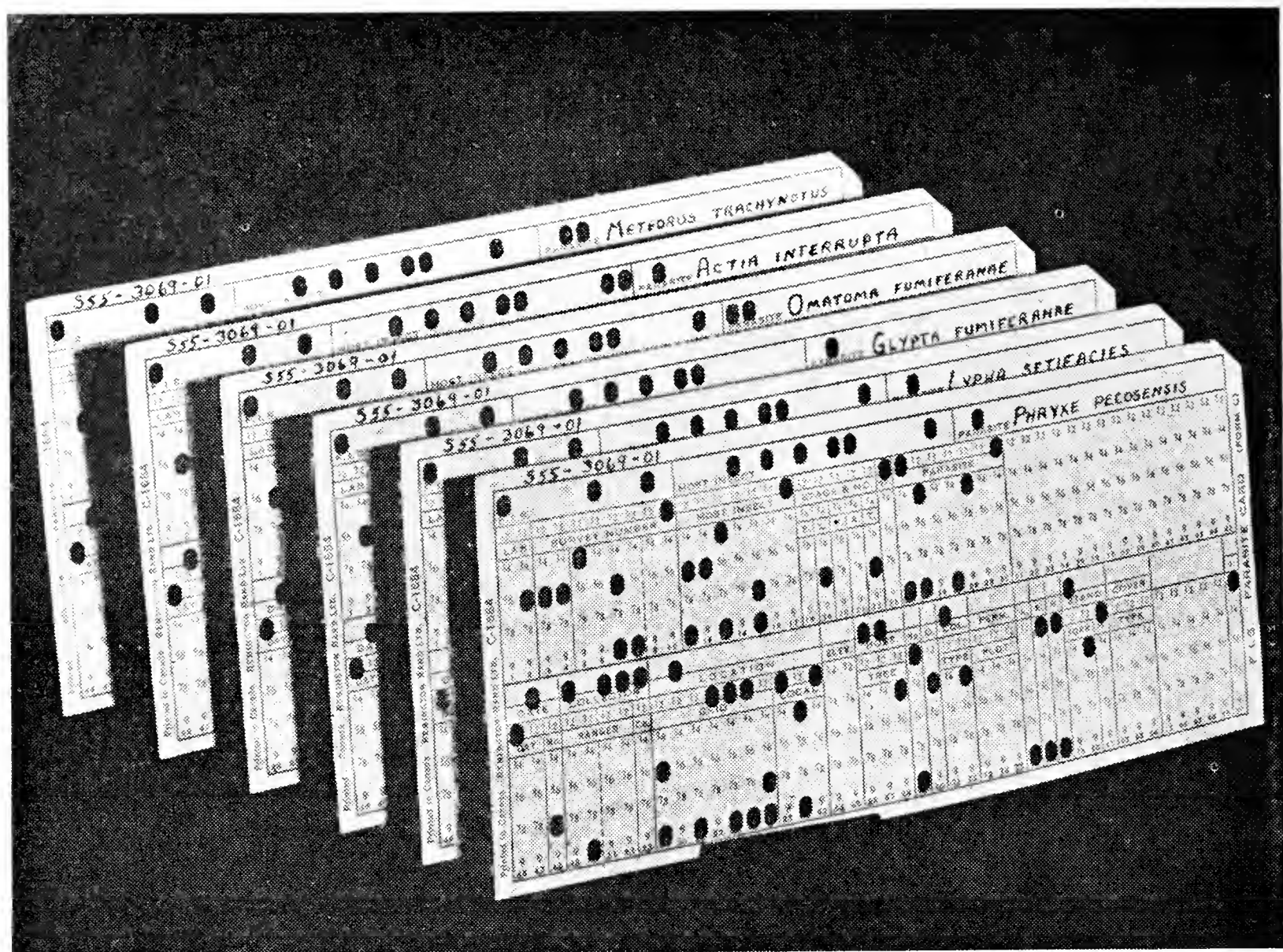


Fig. 7. Series of parasite cards associated with the collection represented in Figs. 3 and 6.

At the close of the field season, each region supplies Divisional Headquarters with a brief factual statement and suitable maps dealing with the major insect problems of the area. These are combined into the Report of the Forest Insect and Disease Survey which is published annually and has a wide circulation both within and outside of Canada. Each ranger is required to prepare in some detail a report of his activities and the insect conditions in his district. These annual reports are prepared in multigraphed form and distributed to provincial and industrial officials during the late winter. In addition to the above formal methods, rangers and Survey officers distribute a good deal of information on insect conditions during the course of their travels and in handling the considerable volume of special requests for information that are processed each year.

All the above methods are concerned largely with the detection and advisory services of the Survey. Research contributions are made to scientific journals by Survey officers. The number of such papers has been increasing and will continue to do so. They have dealt with a wide variety of topics, for example — climatic effects on the spring emergence of the forest tent caterpillar (Blais *et al.*, 1955); larval studies and descriptions of various geometrids (McGuffin, 1956), the spruce budworm (McGugan, 1954), pine root-collar weevil (Watson, 1955), aspen blotch miner (Watson, 1956) and certain sawflies (Wong, 1955); life history studies of the large aspen tortrix (Prentice, 1955), spruce needle miner (Cumming, 1954), and the aspen blotch miner (Martin, 1956); sampling techniques for the winter moth (Reeks, 1956); new species of Coccinellidae (Watson, 1954); parasites of the larch sawfly (Lejeune and Hildahl, 1954) and spruce budworm (McGugan, 1955); detailed morphology of adelgids (Underwood, 1955); laboratory techniques (Ross and Harvey, 1954; Lindquist, 1956); and regional checklists (Ross and Evans, 1956). A number of major contributions are approaching publication and reference has already been made to the national Lepidoptera compilation that is in preparation.

### CONCLUSION

In closing, I should like to say that we are proud of our existing organization and feel that it has progressed considerably from its early beginnings in 1936. We recognize,

however, that we have really only begun, and that progress during the next 20 years is limited only by our imagination and energy. The present account has necessarily been restricted to only the basic procedures and methods of the Survey. Officers are engaged in testing variations and extensions of these in order to improve their value and accuracy. Specialized collection methods to yield quantitative information, improved rearing techniques, streamlining of procedures, and many others are the problems which confront us.

The demand for critical data in connection with large-scale control operations has forced a bias in Survey operations in some regions. To date it has been possible to satisfy these requirements within the existing framework. Recently, however, the need for more satisfactory estimates of insect losses in Canada's forests has been realized. As the Forest Insect Survey will have to accept the major responsibility in this regard, some extension and modification of procedures may be necessary.

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## DISCUSSION

S. A. GRAHAM. The term "forest insect survey" carries a different meaning to various individuals. A number of these viewpoints have been brought out in the series of papers presented this morning: Some have emphasized the biological aspects involving the rise and fall of population numbers. Others have emphasized the appraisal of insect-caused injury. Whereas others have emphasized the detection of incipient or threatening outbreaks before severe injury has occurred. All the speakers have been concerned about techniques through which their objectives may be attained. Furthermore it is evident that a very close connection must necessarily exist between survey, research, and control practices.

The viewpoints expressed stem from the local conditions that have led to the development of each survey organization discussed, and each has its merits. It seems to me, however, that in the interest of clarity we should not lose sight of the differences between them. It may be in order to suggest, therefore, that surveys may be divided into the following categories:

- 1) The biological and population dynamics survey.
- 2) The survey designed primarily to detect incipient outbreaks.
- 3) The survey designed to appraise specific conditions as a preliminary to control operations.

F. P. KEEN. How is the "cycle of abundance" determined for such well known insects as the mountain pine beetle *Dendroctonus monticolae* (Hopk.)?

B. M. MCGUGAN. The recognition of "cycles" for forest insects is a long-term objective of the Canadian Survey. Bark beetles are particularly difficult in this regard and only limited progress has been made. I would like to call on Dr. D. A. Ross who



is in charge of Forest Insect Survey work in the Interior of British Columbia to describe briefly methods of sampling mountain pine beetle populations.

D. A. ROSS. In the past our records of changes in population density of the mountain pine beetle have been empirical over the major portion of the Interior of British Columbia. However, the observations have been supplemented by data from one-chain-wide survey strips run through a few of the areas of chronic infestation. The number of uninfested, "red-topped", and "green-infested", trees on these strips have been counted annually. In addition an annual count has been made of trees killed on one large area north of Merritt. These counts range from a low in 1949 through a high in 1953 to a low in 1955.

J. M. WHITESIDE. How is your survey program correlated with spruce budworm studies in New Brunswick?

B. M. MCGUGAN. Mr. R. S. Forbes who is in charge of Survey activities in New Brunswick is here and will be able to give you a more detailed reply than I.

R. S. FORBES. A high degree of co-operation exists between the Survey and the Green River and Aerial Spray projects. In recent years the Survey has used many sampling techniques that have been developed or refined by Drs. Morris and Webb. I think the role played by the Survey in detecting the numbers and locations of the spruce budworm in the early years of the present outbreak was significant. The distribution and numbers of collections from 1945 to 1949 were plotted on maps in the annual reports of the Survey for these years and showed that the area from which samples were taken extended gradually from the northwestern part of the Province in a southeasterly direction. From 1950 the severity of infestations increased and in 1952 spraying operations were initiated. Since that time the Survey has co-operated with the Aerial Spray Project in providing assistance in aerial surveys and plot studies, but its main responsibility has been to assess conditions outside the sprayed areas.

J. J. FETTES. The Survey has been of great value to the Chemical Control Section of the Forest Biology Division by providing information on the location and intensity of infestations.

C. H. BUCKNER. The title of your annual report is "The Forest Insect and Disease Survey". Could you comment briefly on the integration of the disease portion in the survey pattern as a whole?

B. M. MCGUGAN. Since 1951, we have been developing a disease survey counterpart of the Forest Insect Survey. Development of national objectives and methods has been slow largely because of staff limitations. Forest Biology Rangers have been instructed in the recognition and detection of diseases and are submitting collections to regional pathology laboratories. In effect, the field requirements of both surveys are derived from one ranger staff. Integration of programs is through the regional officers-in-charge and their survey leaders.

# Some Aspects of Forest Entomology in Britain

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## ABSTRACT

*This paper briefly discusses the insect problems encountered in British forestry and shows that although they tend to be on a small scale they are of some general interest because of the rather exceptional background of forest type against which they are set. The heavy fellings which had to be made during the two world wars, coupled with the large afforestation programme now being undertaken by the State, ensure that a preponderance of conifer crops of the younger age classes will characterize the British forest scene for some decades. British forest entomologists assume from this that any major insect troubles which may arise will most probably be those connected with the activities of defoliators. Present indications and occurrences support this view.*

*The situation is complicated and its interest enhanced by the fact that much of the afforestation programme is based on the use of exotic tree species. Non-indigenous forest pest species are also present in some number and their future behaviour in Britain is to some extent unpredictable.*

*As examples of the types of problems now being studied, brief reference is made to current investigations on the sawflies associated with conifer crops, and on the pine looper, *Bupalus piniarius* (L.). It is stressed that in approaching such problems long-term intensive studies on population dynamics, even if these have to be carried out on populations of very low density with all the complications which arise therefrom, hold out the best hope of reward.*

## INTRODUCTION

The problems of forest entomology in Britain, although by no means as serious or commanding as those of some other lands, are of interest because of the rather unique background of forest estate and of forest policy against which they are set. These, in their turn, affect both present day insect problems and current lines of investigation and will undoubtedly influence future developments in this field.

Great Britain is a poorly forested country, only some 6.5 per cent of its surface carrying tree crops. Prior to the 1914-18 war the United Kingdom had no forest policy, and at that time some 97 per cent of the 3 million acres of woodland present in the country was in private ownership. During the war period home-grown timber supplies were exploited and the substitution of home-grown for imported timber effected substantial economies in shipping. As a result of this experience, approval was gained for a forest policy, which included a programme of State afforestation, and in 1919 the Forestry Commission was established as the forest authority. In the inter-war period the Commission acquired a considerable forest estate and by the end of 1939 some 434,000 acres of it were under woodland. Wholesale exploitation of British forests recommenced in 1939 and again continued throughout the war period. In 1943 H. M. Forestry Commissioners produced a report on post-war forest policy (1) and the proposals contained therein now direct the forest programme in this country.

In brief, the main proposal is that 5 million acres should be devoted to systematic forest management and that this target should be secured by the end of the century. It is anticipated that this area of fully productive forest shall be provided by the afforestation of 3 million acres of bare ground and by the improvement of 2 million acres of existing woodland. It is true to say that the State is responsible for the vast bulk of the afforestation programme.

The proposals envisaged that in the first post-war decade 1,100,000 acres would be either replanted or afforested. By the end of the forest year 1954, the Forestry Commission had achieved 64 per cent of its programme to date. In that year 70,400 acres were planted and this figure is stated to be the peak — for the time being — of the Commission's afforestation effort. After 1954 the annual planting programme will decrease primarily because plantable ground is becoming increasingly difficult to



acquire. The 1955 planting programme, however, brings the Commission's forest area up to and beyond the 1 million acre mark (2).

### TYPE OF FOREST CROP IN BRITAIN

Two complementary factors dictate that the afforestation work in this country will be carried out almost exclusively with coniferous tree species. These are, firstly, that the climatic and soil influences on the rough grazing lands — the only land areas at all readily available for afforestation — are such that only conifers can be grown on them as economic forest crops. Secondly, softwoods constitute some 94% of the country's timber requirements and consequently their production must be preferred.

Many areas in Britain are well-suited, climatically and otherwise, to the production of conifer crops and good growth rates are often obtained with many species. In this situation it is interesting to reflect that only one indigenous timber-producing conifer, the Scots pine *Pinus sylvestris* (L.), exists in the country and that most of the afforestation programme is achieved by the use of exotics. For example, by 1947 almost 50% of the plantations formed by the Commission were of the two spruces, Norway spruce (*Picea abies* (L.) Karst.) and Sitka spruce (*P. sitchensis* (Bong.) Carr.); Scots pine represented 21% of the total; Corsican pine (*P. nigra* var. *calabrica* (Loud.) Schneid.) 7%; European larch (*Larix decidua* Mill.) and Japanese larch (*L. leptolepis* (Seib. & Zucc.) Murr.) 6% each; Douglas fir (*Pseudotsuga taxifolia* (Poir.) Rehder) 5%; and other conifers such as *Pinus contorta* (Dougl.), *Abies grandis* (Lindl.), *Thuja plicata* (D. Don.), and *Tsuga heterophylla* (Raf.) Sarg. totalled about 1%; whilst only about 7% of the total was composed of broadleaved trees, mainly oak and beech (3).

The second main feature of British forest crops is the very great abnormality of distribution of the age classes. The proportion of older crops is now very low because of the heavy inroads made into them by the fellings of the two world wars. Although efforts are being made to preserve those that remain, the British forest scene for some time to come will feature this scarcity of mature or near mature stands. Furthermore, the big afforestation and replanting schemes which are being prosecuted in the first two post-war decades ensure that the bulk of the forest area in Britain will be represented by younger and middle-aged crops.

Thus, to sum up, it is obvious that our insect problems, such as they are, are now and will for the next twenty or thirty years be viewed against a background of a rapidly expanding forest area, characterized in the main by the presence or formation of younger conifer plantations, some of them of large extent and many of them showing a tendency towards monoculture because of the restrictions imposed by site conditions, and composed in many cases of exotic tree species.

### PREVIOUS EXPERIENCE

Taking the broad view, the history of the private woodlands and of the more recently formed State forests has shown a rather remarkable freedom from serious insect attack. Certainly, although many insect occurrences have given rise to concern, there has been no incident in Britain which can be thought of as catastrophic in the sense or on the scale of the forest insect epidemics which are known from parts of the European and American continents.

In examining the conditions of the first half of the present century it is easy to detect a limited number of situations which had serious results or which threatened to do so. Firstly, the period from 1906 to 1913 was notable for the infestations, centred in North Wales and northwest England, of the large larch sawfly, *Pristiphora erichsonii* (Htg.). The reports indicate that the attacks were severe enough and sufficiently prolonged to produce tree death and in some instances fairly extensive fellings of larch crops had to be made. The epidemics collapsed naturally in 1913 when parasites (mainly *Mesoleius tenthredinis* (Morl.)), various predators, and what was thought to be a virus or bacterial disease all intervened. Secondly, the logging operations in the two world wars led to upsurges in populations of the pine shoot beetle, *Myelophilus piniperda* (L.), and the large pine weevil, *Hylobius abietis* (L.). These are more truly, of course, managerial rather than entomological problems and the severity of their

effects was mitigated by the normal practices of rapid extraction and delay in replanting. Thirdly, the rapid afforestation by the Forestry Commission of large areas of the East Anglian brecklands with almost pure pine crops led to insect troubles, mainly from the pine sawfly, *Diprion pini* (L.), and the pine shoot moth, *Rhyacionia buoliana* (Schiff.). The attacks of these species are, of course, linked in the main to the age of the crop so that they were transient in nature. However, at the time, the infestations were sufficiently intense to place the future of these plantations seriously in doubt. Apart from the hand collection of sawfly larvae, no large-scale artificial control measures were attempted. The sawfly infestations collapsed naturally, and the crop damage produced by the pine shoot moth has been largely rectified by careful subsequent tending and thinning.

Apart from these highlights, many minor attacks occurred on a variety of crops at all stages of development but they neither merit individual description here nor affect the main statement of the position.

It must not be thought that the relative immunity from attack which British forests have experienced is attributable, entirely or in large measure, to the fact that exotic tree species have been imported without the pests associated with them in their native habitat. The main European conifers, European larch and Norway spruce, have been present in Britain since before 1629 and 1548 respectively and they both now in their new home support a large, varied, and imported fauna. One can mention, as examples, the many sawfly species and the various adelgids associated with these trees. Many of the American conifers were imported into Britain just over a century ago (Douglas fir in 1827, Sitka spruce in 1831, *Tsuga heterophylla* in 1851, and *Pinus contorta* about 1855) and some of their associated insects are present here too. For example, the Douglas fir seed fly, *Megastigmus spermotrophus* (Wachtl), frequently causes heavy seed losses in that species and *Adelges cooleyi* (Gill.) is very common on most Douglas fir crops although it is much less frequent on its alternative host, Sitka spruce. A great number of the most damaging American forest insects, however, such as the spruce budworm, *Choristoneura fumiferana* (Clem.), and the hemlock looper *Lambdina fiscellaria* (Guen.), to say nothing of the bark beetles, are still absent from Britain. In this respect, the trade between the New World and the Old has been rather onesided and disadvantageous to our hosts at this Congress.

The dangerous indigenous fauna associated with our Scots pine has widened its tastes to embrace the exotic pines now grown here. For example, *P. contorta* is now preferred over Scots pine by the sawfly *Neodiprion sertifer* (Geoffr.). Some imported insects have also expanded their fields of host choice; for instance, Japanese larch is now at least as frequently attacked by some of the defoliators from the continent of Europe as is the longer established European larch.

In only one instance has the importation of an insect pest prevented the silvicultural use of a tree species in this country. The common silver fir, *Abies alba* (Mill.), a very desirable species, cannot now be grown in Britain because of the crippling attacks of the silver fir adelgid, *Adelges nusslini* (Borner).

At the present time an import prohibition order (4) operates against all living plants in the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Sequoia*, *Thuja*, and *Tsuga*, and it is hoped by this means to prevent any further additions to the list of injurious insects associated with them.

Although our past history in respect of insect damage to forest crops has been favourable it should not be assumed that all foresters in Britain view the future with complete equanimity. The relative absence of serious infestation in the past is commonly attributed to the vagaries of our climate and to the fact that woodlands have usually been of small extent and composed of a good number of species. The latter condition is undergoing rapid change, as has been shown, and the insect risk attendant on the formation of large areas of even-aged conifer plantation composed of relatively few species are obvious. These risks, from both pests and diseases, have been appreciated and have been accepted. It would be nonsensical to delude ourselves into thinking that we may not run into trouble in the future but British foresters have

had to balance this nebulous threat against the overwhelming needs of rebuilding the country's forest and timber reserves, and the obviously correct decision has been made.

To deal with present insect problems and possible future developments the Forestry Commission maintains an entomological staff, six in number, at its research station. Three of these are graduates, either in forestry or in zoology, and three are non-graduates. In addition, a certain amount of assistance is given by university staffs. As a working hypothesis, the Forestry Commission research staff believes that, in view of the type of forest stand now being created, any major insect troubles in the future are most likely to be those concerned with the activities of defoliators in coniferous plantations. We have already had some hints and indications that this may well be the case. Accordingly, emphasis is being placed on forest insects of that general type, whether or not they are at present of pest status. This seems an appropriate point to refer to and describe some of the current lines of investigation in Britain.

### CURRENT WORK

When one looks at the list of forest defoliators, present in Britain and of possible importance, it is quickly seen that the assembly is a formidable one. Of those known to cause serious damage on the continent of Europe or elsewhere one can mention such lepidopterous species as the pine beauty, *Panolis griseovariegata* (Goeze), the pine looper, *Bupalus piniarius* (L.), the nun moth, *Lymantria monacha* (L.), and *Semasia* (*Eucosma*) *griseana* (Hbn.); whilst numbers of damaging sawfly species are present on pine, larch, and spruce crops. At the present time the conifer sawflies and the pine looper are the subjects of study.

**THE CONIFER SAWFLIES:** Although some, at least, of the pine sawflies are indigenous, those feeding on the larches and the spruces are, like the trees themselves, all of foreign origin. In commencing a study of this group it was obviously of prime importance to ascertain in the first instance precisely what species were present; and secondly to attempt to assess their forest status in their new habitat. The results of this preliminary survey of the position are of some interest.

Seven species of sawfly are now known to occur on larch in Britain, and it is interesting that a by-product of the general review has been the recognition of two new species. The group now includes *Pristiphora erichsonii* (Htg.), *P. laricis* (Htg.), *P. wesmaeli* (Tisch.), *P. glauca* (Bens.), *Anoplonyx destructor* (Bens.), *Pachynematus imperfectus* (Zadd. & Brisch.), and *Cephalcia alpina* (Klug.). It is curious and instructive to note that by far the most commonly occurring species is *A. destructor* which was first described in Britain. In this case the importation into a new locality has resulted in a very distinct change in status. No member of this genus has been recorded as a forest pest on the continent of Europe and *A. destructor* itself is known elsewhere only from Finland where it is very rare, yet in this country most larch crops harbour the species and in certain localities, such as central Scotland and the Welsh border country, heavy infestations recur year after year. Fortunately the impact of these infestations on the crops is not serious. The bulk of the feeding takes place late in the season, just before natural leaf fall, and larch in any case always shows good recovery from defoliation. Of the other species, *P. erichsonii* has already shown its damaging potential in Britain and *P. laricis* is fairly common; the remaining species are of much lesser importance.

The numerical status of the more important species is reviewed at regular intervals by country-wide surveys. Simple sampling techniques — the counting of larval clutches of the large larch sawfly on sample areas, and the jarring of small larch sawfly larvae from sample branches on to a sheet — are used to detect the major changes in population and act as warning indicators.

On spruce crops nine species of sawfly are now known to occur in Britain. These are *Pristiphora abietina* (Christ.), *P. compressa* (Htg.), *P. saxeseni* (Htg.), *P. ambigua* (Fall.), *P. amphibola* (Forst.), *P. subartica* (Forssl.), *Gilpinia hercyniae* (Htg.), *Pachynematus montanus* (Zadd. & Brisch.), and *P. scutellatus* (Htg.). Amongst these, the two bud inhabiting species, *P. ambigua* and *P. amphibola*, are common but of little significance. *P. abietina*, which feeds mainly on current year's needles, is also frequent

and is sometimes important in Sitka spruce crops suffering defoliation of the old needles from the attacks of the green spruce aphid, *Neomyzaphis abietina* (Walk.). The great damage caused by *G. hercyniae* following its introduction into Canada leads us to regard this species with caution even although at the present time it is of infrequent occurrence in Britain. The remaining species on spruce are of little importance.

Of the eleven sawfly species associated with pine in Britain only two, *Diprion pini* (L.) and *Neodiprion sertifer* (Geoffr.), are forest pests. Typically, both infest young stands of pine of under 10 feet in height causing a reduction in height increment but seldom tree death. The outbreaks do not usually persist for more than two or three seasons. Parasites play their part in these collapses and the well-known virus disease of *N. sertifer* often intervenes.

THE PINE LOOPER, *Bupalus piniarius* (L.): The initiation of the studies on this insect in 1952 followed the general policy of investigating those species which although not necessarily past or current pests were obviously of some potential menace. The first epidemic in Britain of the pine looper, which was noted in 1953, lent impetus to this line of work and brought about the first aerial spraying operation against a forest defoliator in this country. Simultaneously, pupal sampling methods to provide population indices have been evolved and for the last three seasons all pine stands in Britain considered liable to attack have been surveyed. The area covered by the annual survey is approximately 86,000 acres.

The pine looper is, of course, a well-known pine pest of pole stage and older crops on the continent of Europe. Most aspects of its biology are recorded but there is very little reliable information on the factors governing population fluctuations. Nonetheless, extensive pupal surveys do record changes in population even if they cannot detect the factors motivating them, and are thus of definite value in drawing attention to upward trends and, in extreme cases, of allowing control schemes to be planned in good time. In Britain, the standard method for pupal counting consists of the examination of five quadrats, each measuring one yard square, per compartment of forest — i.e. per 25 to 30 acres approximately. These quadrats are spaced equidistantly along a transect traversing the compartment. The sampling yields a population index which is expressed as the number of pupae per square yard of forest floor. The very low sampling fraction, which allows of large forest areas being surveyed with the minimum of effort, is permissible and gives acceptably accurate results mainly because the distribution of the pupae of *B. piniarius* is fairly uniform within a stand. Using a sample of five quadrats per compartment, the standard error of the mean is about 25% of the mean number of pupae per square yard. Counting on twenty-five quadrats per compartment would only reduce the standard error of the mean to about 11% of the mean number of pupae per square yard. The degree of precision obtained from the method now in use is sufficiently great to detect the main changes in population density which is the prime aim of the annual survey.

The endemic levels of *B. piniarius* population in pine crops in the thinning stages in Britain are of the order of one or fewer pupae per square yard. It has not yet been possible to define what density of pupal population must be reached before crop damage in the following season becomes probable, and in any case the nomination of such a warning index would be highly artificial because of the critical influence of the weather at the time of adult flight and of the early larval stages on the development of the succeeding generation. Populations which approach or reach a density of ten pupae per square yard must, however, be regarded as distinctly abnormal and to some extent threatening.

In the case of the outbreak at Cannock Chase Forest in Staffordshire, just over 100 acres of 31-year-old Scots pine were completely or very severely defoliated in the summer of 1953 and pupal counts made in the winter of 1953-54 yielded average figures of between 150 and 300 pupae per square yard in the most heavily infested areas. Where defoliation was obvious but not as intense as the above, the counts ranged between 40 and 150 pupae per square yard. In the same winter, at Culbin Forest, Morayshire, where many adults had been seen on the wing in 1952 and where the 1952-53 pupal counts had averaged about 3.5 pupae per square yard, the average



count throughout some 3,500 acres of crop was approximately 20 pupae per square yard. No signs of defoliation could, however, be observed at Culbin at this time. Obviously, if further serious crop damage was to be avoided at Cannock Chase artificial control measures were essential, especially as it is common experience that infestations of the pine looper very seldom come under natural control before irreparable harm has been caused to the forest. On the sand dune afforestation area at Culbin, where the crop had been established at great expense and where its continued growth is marginal, it was felt that even some defoliation by *B. piniarius* might well prove critical. Accordingly, a protective and preventive control scheme was also planned for that forest.

The control schemes, which covered 2,500 acres at Cannock and 3,500 acres at Culbin, took the form of spraying from fixed wing Auster aircraft which applied 1 lb. of DDT in 3 gallons of spray liquid per acre. The treatments were timed to coincide with the presence of the early larval stages and to calculate this date observations were made on the timing of adult emergence and on the rate of egg hatching. At Cannock, 88% of the larvae killed by the treatment were in the first instar and 12% in the second. At Culbin, where of necessity the spraying had to be carried out after that at Cannock, 2% were first instar, 73% were second instar, and 25% were third-instar larvae.

The effects of the insecticidal applications were assessed by three methods:—

- (a) by direct counting on sampling trays of larvae killed by the treatment,
- (b) by pre- and post-treatment counting of larvae on sample shoots,
- (c) by pupal counts in the winter following treatment.

All of the results obtained indicate that the applications were effective. For example, in most areas the mortality counts were of the order of 100 larvae per square yard, whilst in the most heavily infested crops at Cannock the kill exceeded 1,000 larvae per square yard. These figures are underestimates since a proportion of the dying larvae remain trapped in the tree crowns on their silken threads. The overall effect of the treatment can be summarized by saying that the population was reduced to normal levels. In both forests, in the winter following treatment, more than half of the compartment yielded zero counts of pupae whilst figures in the remaining compartments were very low. Although the spraying operations themselves can therefore be regarded as successful, some crop loss, quite apart from incremental losses, occurred at Cannock where the weakened defoliated trees were invaded by *Myelophilus piniperda*. Parts of the crop had to be clear felled and very heavy thinnings had to be made in other areas.

Now that these outbreaks have been dealt with and that the annual pupal survey is in operation to keep a check on developments, the studies on the pine looper are reverting to the original scheme — namely, that of attempting to gather information on the factors governing the population dynamics of the species. For this purpose sample plots, in which intensive sampling at all stages of the life cycle will be carried out, are being established and it is hoped that the data from the sampling, backed up by direct observations, may indicate what influences are important in maintaining stability or in initiating fluctuations in population density. No results are yet available from these studies nor can they be expected for some years since many difficulties of sampling technique at low population levels have yet to be overcome. Even if in the long run only the most general of trends are indicated it will be a step in the right direction. At the present time knowledge of this subject is almost entirely lacking. For example, it has as yet been impossible to explain why the epidemics at Cannock and Culbin arose and were accompanied by fairly high levels of population in many, but by no means all, other parts of the country in 1953. The widespread and simultaneous nature of the increases strongly suggests some underlying climatic influence, but examination of the records has so far failed to define what this was. We firmly believe, however, that long-term intensive study, utilizing the best statistical methods now available to us, is the most promising line of approach to the problem.

OTHER WORK: There is no time today to describe in any detail what other forest insect problems are being investigated, but brief mention must be made of the serious



secondary issues which followed the destructive gale of January 1953 in the northeast of Scotland. The storm devastated some 10,000 acres of woodland, mainly Scots pine in the older age classes, and left undamaged most crops of under about 40 feet in height. The pine shoot beetle, *Myelophilus piniperda*, has bred up in large numbers in the blown stands and has caused serious damage to the remaining younger pine crops. Little could be done in the way of controlling this outbreak except to expedite the clearance of the blown timber. On a smaller scale some control was achieved by spraying infested timber in stack with 2% DDT emulsion at the rate of 1 gallon per hundred square feet of bark surface. Although crown pruning deformations are now very severe in the younger crops it is at least fortunate that no large scale breeding in standing trees has occurred despite the very high levels of beetle population which have been reached.

The replanting of the blown areas will be hindered by the activities of the pine weevil, *Hylobius abietis*. This should not be as serious as was at one time anticipated, firstly, because the disturbed blown stumps became rapidly exhausted as breeding sites: and, secondly, because recent experimental work has shown that good and economic protection from pine weevil attack can be given to newly formed conifer plantations by the application of various insecticides as either sprays, dusts, or dips.

### CONCLUSION

It has been possible in this brief paper to indicate only in the most general of terms what is being done in the field of forest entomology in Britain and the background against which this work is set. Although our problems are small-scale ones I trust that this outline description has been of some interest to the audience, even if only to compare with the rather different circumstances and conditions which are being reported to you by other speakers at this symposium.

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# Problems of Forest Entomology in Exotic Forests in New Zealand

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## ABSTRACT

A short account is given of the exotic forests of New Zealand; these consist largely of pine and occupy some 800,000 acres. The principal species is *Pinus radiata* with 540,000 acres; other widely used species are Douglas fir, European larch, Corsican pine, and the southern pines. The concept of ecological balance is developed to illustrate the point that the physiology of any tree is adapted to the ecological factors of its natural environment. When introduced to a new environment a completely new set of climatic, edaphic, physiographic, and biotic factors may be encountered. The successful establishment of an exotic tree depends upon the degree to which these factors differ from those of the native habitat and upon the ability of the tree to adapt itself to the new conditions until a new and stable balance is developed. Of the problems arising during this period of adjustment, forest insects are discussed under the following headings: (1) the primary exotic element; (2) the secondary exotic element; (3) the primary indigenous element; and (4) the secondary indigenous element. A primary insect is defined as one which is independent of any debility within the tree, whereas a secondary species can attack only trees already weakened by some predisposing cause.

Problems of insect control are dealt with under the following heads: (1) silvicultural control, which is shown to be highly desirable but physically and economically impossible under present conditions; (2) chemical control, to meet an emergency arising through the introduction of any destructive insect (the use of aerial spraying to combat an outbreak of an indigenous defoliator is noted); and (3) the value of biological control for indigenous and exotic primary and secondary insects is discussed; examples are given of control measures already attempted.

Finally brief mention is made of ecological and taxonomic problems.

## INTRODUCTION

New Zealand is a small country stretching from latitude 34° S. to 47° S. and located in the southwest of the Pacific ocean. It has a population of about 2 million. The indigenous forest has been largely destroyed and forests of exotic species have been established; as a result the whole forest economy of New Zealand hinges upon some 500,000 acres of *Pinus radiata*.

It is perhaps unfortunate that in New Zealand there is no single entomological problem of outstanding importance in the exotic forests. Although many minor problems which have arisen in the past have been of a temporary nature, it is inevitable that in the future, losses from insect damage must increase. Unless new outbreaks can be recognized and prompt measures taken to combat them, the results may be disastrous. A single important problem now, would serve as a focal point around which staff, equipment, and techniques of control could be built up to the standard recommended by de Gryse (1955) in his report on Forest Pathology in New Zealand.

Indigenous forests in their natural state are reasonably stable except for long-term changes due to climatic factors or to the break-down of the so-called climax association of mature forest. Exotic forests, on the other hand, are vulnerable owing to lack of harmony between tree physiology and the environment (Boyce, 1954). This condition is particularly apparent in the unstable biological balance which renders the forest liable to uncontrolled outbreaks of insect damage. Examples will be given to show how the problems which have already arisen, and those which may be expected to arise, can all be correlated with instability and lack of harmony between physiology and environment.

## THE FORESTS

In round figures the area of exotic forest is about 800,000 acres. These forests are practically all less than 50 years old and have been formed by planting or by regeneration of planted stands. The main species is *Pinus radiata* (D. Don), which occupies over 540,000 acres. The forests are being cut and regenerated at the rate of about 4,000 acres a year, which figure may be expected to rise to 16,000 acres by 1970. Planting of new areas is still proceeding at the rate of 5,000 acres a year.

Except for small areas of Eucalyptus, all the successful species are from the Northern Hemisphere. In their native habitats these trees grow in harmony with their environment and their physiological processes may, at least for periods involving several human generations, be considered to be adapted to the normal fluctuations in climatic, edaphic, physiographic, and biotic factors.

In New Zealand exotic forests are usually relegated to the poorer sites and have in some cases been established up to and beyond the limits of their climatic and edaphic requirements. The range of these species must inevitably be reduced through the intervention of biotic factors, particularly insects and fungi. This applies not only on poor sites but also on some which have given exceptionally good growth in the past but which are outside the true climatic range of the tree which is subject to fungal or insect attack.

Exotic forests throughout the world are notorious for their early promise and ultimate failure; consequently no species can be said to have been successfully established until it has been tested through several rotations. This cautious approach is particularly applicable to *P. radiata*, which must be required to produce the bulk of exotic timber and pulpwood for the next 60 years (Rawlings, 1948). This species should be regarded as a stop-gap until timber requirements can be met by longer rotation exotics, such as Douglas fir, and by native species such as *Nothofagus*.

It is possible that continued use of *P. radiata* may eventually prove to be possible over considerable areas but its future economic range is by no means clear at present.

It is only through full and intensive study of tree physiology and all ecological factors of the habitats that sufficient information can be accumulated to enable foresters to minimize damage and so extend the time during which exotic forests, particularly *P. radiata*, can be maintained at an economic level of production.

Of the ecological factors the biotic will undoubtedly provide the pivot upon which ultimate success or failure will hinge.

## THE BIOTIC FACTORS

The biotic factors of a forest constitute a vast assembly of organisms each occupying an appropriate niche. Here we have an important concept — that of biological balance. Since the draft of this paper was written a paper has come to hand by Graham (1956). Graham develops much the same theme as is presented here but uses the term "Law of Natural Compensation" to illustrate the causes of instability in natural forests and in plantations of native species.

To the forester this concept centres round the tree or, more correctly, round so many acres of trees. Under conditions of biological balance, or natural compensations, although the numbers of any organism of a forest (including the tree or trees) are in a state of continual flux, the numbers fluctuate about a mean through the action of natural controlling agencies. The greater the number of factors, in species, the more stable should be the balance. Under natural conditions only one seed from a mature tree can, on the average, give rise to another mature tree. This enables natural selection to operate in many directions. By way of contrast, in the establishment of an exotic forest natural selection is largely eliminated and trees which are genetically undesirable or weak are likely to be utilized.

In a balanced forest trees can be killed by insects only after they have been weakened by competition, defoliation, climatic conditions or other factors. When a natural forest is put under management, the forester appoints himself as the dominant ecological factor. His success will depend largely upon how closely he can work in harmony with natural conditions. Every change he makes in the environment and

every control he attempts to impose will necessitate further changes or controls to maintain the new balance within the forest. Upsetting the biological balance may result in heavy economic losses before a new balance is established.

In newly established exotic forests there is only an unstable and inadequate biological balance, and in addition the trees may be required to adapt themselves to an entirely new set of environmental conditions. Normal killing agents are absent and competition for soil-room and water may become intense. As a New Zealand example *P. radiata* may be considered. This species, introduced from California, was required to adapt itself to a new climate, to soils lacking the necessary mycorrhizal fungi, to physiography often entirely dissimilar and with the normal biotic complement entirely absent. In addition it was subject to competition from native vegetation and possible attack by native insects and fungi, to which it had no inherent resistance.

Historically we know that *P. radiata* flourished in its new habitat; suitable mycorrhizal fungi were introduced and the trees showed phenomenal volume and height increment. Some facultatively parasitic fungi were introduced which caused damage in unfavourable localities. The early stands suppressed the native vegetation and became practically pure *P. radiata* forest. Gradually native insects and fungi colonized this forest and a number of exotic species were introduced. Because the trees were planted at spacings of 6 by 6 and 8 by 8 feet, competition soon became severe and resulted in mutual suppression of all the trees. Suppression was relieved to some extent through unequal growth, tending towards the production of dominants, but an extremely dangerous condition developed in which the trees would have been most susceptible to any primary destructive organism which might have been introduced. However, this condition has now been adjusted through the action of a secondary exotic insect, *Sirex noctilio*, which reduced the stocking with great benefit to the health of the remaining trees.

In dealing with the entomological factors it is not proposed to attempt any precise division into destructive and beneficial species, but rather to consider all insects as factors in maintaining the biological balance. When considering control measures however, it is convenient to separate those insects capable of causing severe damage or mortality in the forest. Such insects are considered as primary if their attack is independent of any predisposing debility within the tree. Secondary insects, on the other hand, require that some other factor shall have rendered the tree susceptible to attack. It is necessary when considering control measures to distinguish between exotic and indigenous insects.

The Primary Exotic Element contains species which are potentially the most destructive and which are capable of doing very considerable damage. Defoliating Hymenoptera and Lepidoptera are particularly dangerous and constant watch must be kept to detect newly established species. Of the important primary species, none has yet become established which is capable of doing any great damage to existing forests, although in the past some have influenced the selection of species. *Pineus borneri* (Ann.) was formerly prevalent on *P. radiata* but is now controlled by the introduced agromyzid *Leucopis obscura* (Hal.). The spruce aphid *Elatobium abietinum* (Walk.) and the spinning mite *Paratetranychus ununguis* (Jacobi) caused serious damage and contributed to the disuse of the spruces as forest trees. Similarly a number of defoliating Coleoptera, introduced from Australia, have contributed very largely to the disuse of *Eucalyptus globulus*. *Hylastes ater* (Payk.) may be an important factor in preventing the reproduction of pine in localities where natural regeneration is scanty.

The Secondary Exotic Element contains species which could prove dangerous owing to the lack of ecological balance within the forest. Included here is *Hylastes ater* (Payk.), which is normally a harmless secondary insect in logs and stumps. *Hylastes* can attack the cambium of weakened trees, acting as a typical bark beetle, and may become an important primary in that the migrating adults destroy regeneration. *Sirex noctilio* (Fabr.) is an outstanding example of a secondary insect capable of causing extensive destruction of living trees. This species is the vector of a facultatively parasitic fungus, probably an undescribed species. The fungus is deposited with the eggs in the stems of living pines and is capable of killing trees weakened by overcrowding. During the 1946-49 drought period, 30% of the *P. radiata* was killed in



this way over some 400,000 acres. The *Sirex* outbreak was a reflection not only of the unhealthy state of the stands but also of the absence of more aggressive species which would have eliminated unhealthy trees before they reached the stage suitable for *Sirex*.

The Primary Indigenous Element contains numerous native defoliators, any of which is liable to become epidemic. The most serious outbreak so far recorded was of the boarmid, *Selidosema suavis* (Butl.), which caused severe to complete defoliation over some 8,000 acres of *P. radiata* in 1952. Other species damaging *P. radiata* are tortricids and the psychid *Oeceticus omnivorus* (Fered.). Fortunately these species are followed to their new host by their parasites, and outbreaks are soon brought under control. Other species include the cerambycid *Navomorpha lineatum* (Fab.) which has become of some importance in Douglas fir stands. Damage is caused by the larvae which bore into and girdle branches and leaders. The chrysomelid *Eucolaspis brunnea* (Fab.), periodically causes defoliation of *P. radiata* and other trees. Various species of scarabaeid beetles act in a similar manner.

The Secondary Indigenous Element contains species which have as yet done no damage to exotic forests. They have however given some trouble by damaging forest produce during extraction. Much of the established forest will become overmature before it can be utilized so that damage by insects of this group may be expected in the forest at a later date.

### CONTROL MEASURES

The selection of appropriate control measures will depend largely upon the correct determination of the type of insect. Once it has been decided that control should be attempted the measures to be adopted will be broadly as follows:—

For a primary exotic insect: chemical control until biological control can be secured.

For a secondary exotic insect: silvicultural control with biological control as an ultimate refinement. Chemical control may be used to protect forest produce.

For a primary indigenous insect: Chemical control if absolutely necessary to check an outbreak until the balance can be restored naturally. The use of viruses may be considered.

For a secondary indigenous insect: Silvicultural control. Chemical control may be applied to protect forest produce during extraction and seasoning.

**CHEMICAL CONTROL:** The control of a forest insect by aerial spraying was attempted in New Zealand for the first time in 1951. The spraying was undertaken to check an outbreak of the primary indigenous insect *Selidosema suavis*. Some 6,000 acres were treated with excellent results. The experience gained will prove to be of the utmost value should it be necessary to combat a newly introduced primary exotic insect and keep it in check until biological control is secured.

In the forests chemical control should be applied only against a primary insect and only if it becomes necessary to reduce their numbers to prevent mortality. Chemical control is used also to prevent grass grub damage in nurseries and to protect forest produce. As a precautionary measure it is considered that sufficient chemical should be available to treat 10,000 acres of forest, and that it should be possible to commence spraying at a week's notice.

**SILVICULTURAL CONTROL:** The lack of ecological balance in exotic forests, particularly the absence of normal killing agencies, makes it imperative that the forester should maintain his position as the dominant ecological factor and carry out regular thinning and other silvicultural operations. In this country, however, it is economically impossible, at present, to give the forests the attention necessary to maintain them in a healthy condition. As a consequence outbreaks of secondary insects may be expected. These outbreaks may cause mortality beyond what is thought to be desirable. The consequences may be disastrous should a bark beetle become established in overmature forests of a species such as *P. radiata*.

The conversion of large areas of even-aged forest into an appropriate series of age classes under sustained yield, the treatment of regeneration, thinning practices, and choice of species are all problems which have to be met.

The way in which these problems are dealt with will, very largely, determine the entomological problems which follow. Conversely the entomological problems will, to some extent, dictate the silvicultural principles to be followed.

The effect of various silvicultural practices upon the insect population is not only unpredictable but may vary from year to year due to climatic changes. Silvicultural operations during the summer months, particularly in dry years, have been shown to bring about an increase in *Sirex* damage. The main problem here is to forecast the effect of any silvicultural measure and to formulate modifications at once economically feasible and effective in minimizing insect damage.

**BIOLOGICAL CONTROL:** Biological control is normally effective only against primary insects. Indigenous parasites have followed indigenous hosts to their exotic food plants, but cases may occur where this fails to happen, and it may be necessary to search for new parasites from overseas countries. New parasites may also be found which will give more effective control than is being exercised by the normal parasites.

It is in the control of primary exotic insects that there is the greatest scope for biological control. In the event of a dangerous species becoming established it would first be necessary to apply chemical control methods. This, however, would soon become too expensive to be economically possible and control by insect parasites and predators or by fungal or virus disease must be established with a minimum of delay.

In the field of biological control there is much to be learnt about the role of alternate hosts of parasites and the provision of their food plants may be possible. Another promising field for study is the feeding habits of adult parasites. A young pine forest contains no flowers and, in New Zealand, scale insects on pine are rare. In older forests more flowers occur and honey dew is produced on ferns and other plants. A detailed study of the value of various plants in providing food for parasites would seem well worth while. A study of virus diseases of insects is urgently required; their value being amply demonstrated in the collapse of the *Selidosema suavis* outbreak in 1952. This was brought about by a virus disease which wiped out the caterpillars in unsprayed areas only a few weeks after chemical control on sprayed areas had been secured.

Many parasites have already been introduced. Of the primary exotic insects *Pineus borneri* (Ann.) appears to have been controlled by the introduced agromyzid *Leucopis obscura* (Hal.). An attempt is now being made to establish *Amblymerus apicalis*, a parasite of the Douglas fir seed chalcid, *Megastigmus spermotrophus* (Wachtl.). A few were liberated in 1955 and, with a bumper seed crop, prospects for their establishment appeared good. Larger numbers were reared in 1956 but the almost complete failure of the seed crop made their establishment very uncertain. This illustrates one of the limitations of biological control where the host is controlled by fluctuations in food supply.

Among the parasites of secondary insects, *Rhyssa persuasoria* (L.) has been established on *Sirex*, and *Ibalia leucospoides* (Hochenw.) is now probably established on the same host. Large areas of one age group, particularly if untended, permit and induce wide fluctuations in the numbers of secondary insects. The use of parasites under these conditions is practically worthless but may ultimately prove of value when improved silvicultural practices are adopted.

## CONCLUSION

The forest insect problems which have already been met in the exotic forests of New Zealand have presented little difficulty in themselves. Preventive measures in the form of quarantine inspections appear reasonably effective. Detection is covered by a recently organized Biological Survey. Chemical and biological control facilities are inadequate, but are capable of rapid expansion to meet an emergency. Silvicultural control methods can only be applied over a long period, and lack of adequate silviculture constitutes the greatest danger from secondary insect damage to the forests. The introduction of a dangerous primary insect is undoubtedly the greatest hazard.

Taxonomy presents a considerable problem and identification is frequently impossible. Much work remains to be done in the identification of larval forms and in life

history studies. There is unlimited scope for fundamental research into all phases of forest entomology. Many problems must remain unsolved because entomological knowledge in itself does not provide the answer. Entomology and mycology are very closely inter-related, and few problems can be completely solved until detailed information has been obtained on physiology, bioclimatology, soil relations, and allied subjects.

New Zealand is committed, by past policy, to a forest economy which at present hinges upon a single species — *Pinus radiata*. Whatever improvements may be possible in the future can only be made if production can be maintained for at least the next 60 years in the *P. radiata* stands. Failure of the *P. radiata* stands would mean the collapse of the timber and pulp industries now being built up around the exotic forests. It would also cause continued overcutting of indigenous forests and nullify plans for their perpetuation.

The fundamental entomological problem then is to protect the *Pinus radiata* stands from serious injury, at least until the year 2010, by which time the crisis should have been passed. In view of the extreme hazards inseparable from exotic forests and the proved vulnerability of *P. radiata*, the problem is no light one. In reference to a description of the New Zealand *P. radiata* forests de Gryse (1955) says: "It would be difficult, on purely theoretical grounds, to enumerate a better array of attributes or conditions by means of which a forest vulnerable to insect attack could be characterized". Mr. de Gryse enumerated the requirements of an organization designed to cope with this problem. If these requirements can be met there is every probability that the problem can be solved.

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#### DISCUSSION

R. J. KOWAL. (1) Why is the timber economy of the country dependent upon one species of tree — and it an exotic one? (2) Isn't this a dangerous situation in the event of a tree-killing catastrophe? (3) Why are native species not grown?

C. B. RAWLINGS. (1) A matter of government policy and a large volume production of *P. radiata*. (2) Yes, very. (3) All native species require rotations of 100 to 500 years and regeneration of most is not yet understood.

D. E. GRAY. I wonder if Mr. Rawlings would care to elaborate on how far New Zealand has progressed in implementing the recommendations made by Mr. J. J. de Gryse on forest biology problems of New Zealand?

G. B. RAWLINGS. A good start has been made with the Biological Survey, staff has been increased, and plans for a new laboratory have been secured.

J. D. BLETCHLY. In the United Kingdom and elsewhere considerable difficulties have been caused by the Australian quarantine regulations designed to prevent the introduction of *Sirex* woodwasps. These regulations often involve the exporter in the expense of fumigation by methyl bromide which may be serious in a highly competitive market. I would like to ask Mr. Rawlings whether he has any comments or recommendations on this problem. Mr. Rawlings' work on the association between *Sirex* and fungi is of interest to us since in Europe the situation appears to differ. Is Mr. Rawlings of the opinion that in New Zealand trees are killed primarily by the associated fungus rather than by the woodwasps themselves?

G. B. RAWLINGS. New Zealand also suffers from Australian quarantine restrictions; in my opinion they are justified. It is necessary for the fungus to kill the tree or decay the timber before it can be utilized by *Sirex*. *Sirex* places the fungus in the wood for this purpose.

# Insect Problems in Forest Plantations in Northeastern United States

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## ABSTRACT

*Forest planting in the United States is an operation of major proportions. Up to 1955 a total of 10.7 million acres had been planted, and there are some 50 million "plantable" acres today. In the Northeastern States about 1.8 million acres have been planted and this work is going forward at a rate of about 110,000 acres annually. Up to about 1940 white pine, red pine, and Norway spruce were the major tree species selected for planting; but the ravages of insects, primarily the white pine weevil and European pine shoot moth, have been responsible for a shift in recent years to other tree species. Progress has been made in the chemical control of defoliators, the white pine weevil, and a few other pests. Others such as shoot moths and the recently discovered Matsucoccus scale on red pine have resisted all efforts at practical control by insecticides. Although further research in chemical control is necessary, there is a need for increased emphasis on studies directed toward the development of more permanent types of control. These include biological control with emphasis on insect diseases; control by upsetting biological processes through irradiation; silvicultural control through regulation of species mixture; and development of strains of trees resistant to insect attack. For immediate protection, detection and appraisal surveys are needed to locate outbreaks so that prompt control measures may be taken.*

I would like to begin by giving a few statistics on the forest-plantation situation in the United States. Up to July 1, 1955, nearly 10.7 million acres had been planted, of which 22 per cent were on Federal lands, 16 per cent on other public lands (mostly State-owned), 53 per cent on private lands, and 9 per cent for wind barrier purposes. The present rate of planting, based on records for the past 2 years, is about 800,000 acres annually. There are, according to the Timber Resource Review recently released by the U. S. Forest Service, some 52 million "plantable" acres, of which 9 million are on public lands and 43 million in private ownership.

In the 12 Northeastern States which comprise the New England and Middle Atlantic regions, about 1.8 million acres have been planted, with 1.4 million in the states of New York and Pennsylvania alone.

A few plantations were established in the Northeast during the 19th Century, but forest planting did not become an organized operation until the first decade of the present century. It received a great impetus during the thirties when the Civilian Conservation Corps, an agency born of the depression, organized forestry camps with tree planting as one of its principal functions. At present forest trees are being planted in the Northeast at a rate of about 110,000 acres annually.

The New York Conservation Department has kindly supplied some planting records for that state from 1909 to 1955. These records, I believe, indicate the planting trend for most of the region; and it is interesting to note that there has been a marked change, during this period, in tree species selected for planting. The six species that comprise nearly 95 per cent of the trees planted in New York are white, red and Scotch pine, Norway and white spruce, and Japanese larch. From 1909 to 1928 white pine and Norway spruce accounted for 62 per cent of all trees planted, as contrasted with 23 per cent since 1950. Thirty-two per cent of the trees planted during the thirties were red pine, but since 1950 only 20 per cent were of that species. In contrast, Scotch pine, white spruce, and Japanese larch have become increasingly popular and now comprise 54 per cent of the trees planted as compared to only 17 per cent from 1909 to 1928.

What are the reasons for this shift in popularity of tree species for planting during the past half century?



The ravages of insects have been largely responsible for the reduction in planting of white pine, Norway spruce, and red pine. Scotch pine and white spruce have recently been in demand for Christmas trees and these species, along with Japanese larch, have up to the present time suffered little damage from insects.

White pine is perhaps the most valuable coniferous species in much of the Northeast; and were it not for the white pine weevil, *Pissodes strobi* (Peck), it would be the most favored species for reforestation today. Open-grown plantations provide optimum conditions for weevil attack, and many plantations have been virtually ruined. In some stands over 90 per cent of the trees have been weeviled one or more times, leaving the trees crooked or forked and of little value.

Norway spruce is so severely attacked in some areas that it is no longer being planted. White spruce as well as red and Scotch pine, are relatively free from the ravages of this pest.

A serious pest of seedling white pines is the Pales weevil, *Hylobius pales* (Hbst.). It also attacks seedling red pines and other conifers. This pest invariably appears when pines are planted in recently cut-over or burned-over pine areas. It is capable of killing a high percentage of the seedlings.

There is at present a widespread outbreak in the Northeast of the pine leaf aphid, *Pineus pinifoliae* (Fitch), in white pine stands that are growing in the vicinity of spruce, the alternate host of this insect. Many small pines have been killed, but damage to spruce has been negligible. The pine spittle bug, *Aphrophora parallela* (Say), is a potential enemy of white pine, as well as red and Scotch pine. Among the defoliators are a number of sawflies both native and introduced that are capable of causing damage. White pine cones are often severely damaged by insects.

More red pine was planted in the thirties than any other conifer. In its native habitat in the northern part of the region, red pine is almost an "insect-free" species. It looked like the ideal species for reforestation. But the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) found a most desirable food plant in red pine. Where the winter temperatures were not too low it caused severe damage. In some parts of the region the planting of red pine has been completely halted because of this pest.

In the southern part of the region the native Nantucket pine tip moth, *Rhyacionia frustrana* (Comst.), is beginning to invade red pine plantings. This tip moth is a very serious pest in plantations of loblolly pine in Delaware and Maryland. Damage by these shoot and tip moths is especially severe in young plantations. Growth is retarded and trees become stunted and deformed.

Among the defoliators of red pine, sawflies and the pine looper have occurred in epidemic numbers. The native sawflies, *Neodiprion lecontei* (Fitch) and *N. nanulus* (Schedl) have defoliated large acreages. The introduced *N. sertifer* (Geoff.) has caused widespread defoliation of red pine plantings in New Jersey and is now invading stands in Connecticut and New York. Another foreign species, *Diprion frutetorum* (F.), has caused heavy feeding in red pine stands in Connecticut. The native pine looper, *Lambdina athasaria pellucidaria* (G. and R.), stripped a plantation near New Haven, Conn., last summer. When red pine stands are thinned, outbreaks of *Ips pini* (Say) sometimes develop. But even in the absence of thinning this insect may be troublesome. For example, there are now several red pine plantations in Massachusetts where groups of trees have died, apparently from *Ips* attack. These stands had not been disturbed by cutting. Factors such as drought and excessive hot weather appear to cause outbreaks of *Ips*, particularly in stands on heavier soils.

A pair of spittle bugs, *Aphrophora saratogensis* (Fitch) and *A. parallela* (Say), are potential enemies of red pine and have caused severe damage in other regions.

And now a new insect pest of unknown origin, but suspected of being foreign, has appeared within the past decade. I refer to the red pine scale, *Matsucoccus resinosae* (B. and G.), which is potentially the most serious red pine pest of all. It is known to occur only in one small area in Connecticut and two spots in southeastern New York. But in these areas it is killing trees at an alarming rate.

Up to the present time white spruce, Scotch pine, and Japanese larch have not suffered extensive damage from insects. There are, however, a number of potential



enemies; and it would be unwise to assume that these tree species are permanently safe. The European spruce sawfly, *Gilpinia hercyniae* (Htg.), is known to occur in white spruce plantations. Scotch pine is subject to attack by many of the enemies of red pine and is particularly vulnerable to damage by the root crown borer, *Hylobius radicis* (Buch.). The larch sawfly, *Pristiphora erichsonii* (Htg.), and the larch case bearer, *Coleophora laricella* (Hbn.), are well known defoliators of larch.

What are the possibilities of controlling these insect enemies of plantations? A great deal of research has been conducted in the field of chemical control to screen insecticides and develop methods for applying them.

Considerable success has been attained in controlling white pine weevil adults in early spring by spraying the leading shoot of white pine with concentrated lead arsenate or DDT spray with a knapsack sprayer equipped with an extension rod. This method is feasible for treating small areas where the trees are under 12 feet in height. Nearly 100 per cent control of the weevil can be obtained by this method. Studies are now under way to determine if it may be possible to apply sprays in the fall that will give effective control the following spring. Weather conditions in the Northeast are much more favorable for spraying in September and October than in March and April.

For larger areas aerial spraying with DDT will give a high degree of control. By applying 2 pounds of DDT in 2 gallons of spray per acre with a helicopter or 4 pounds of DDT in 4 gallons per acre with a fixed-wing airplane, over 95 per cent control of the weevil is possible.

It is possible to control Pales weevil adults by applying heavy dosages of concentrated lead arsenate or DDT sprays to seedling pines in nurseries or after they are planted or by dipping the bundles of seedling in these spray mixtures.

Most of the defoliators are relatively easy to control, when the larvae are feeding, by aerial spraying with 1 pound of DDT in 1 gallon of spray per acre.

There are special, but rather expensive, chemical treatments that are fairly effective for control of the pine leaf aphid, root collar weevil, and *Ips*.

Intensive research in the chemical control of shoot and tip moths and the *Matsucoccus* scale has thus far failed to produce a practical method for control of these pests in forest plantations.

Research in chemical control must continue; and where economically feasible, efforts should be made to prevent damage from insects through spraying. But it is important to recognize that chemical control is only a palliative. The stands remain as susceptible to another outbreak as before; and it is usually only a matter of time before control operations must be repeated. Thus entomologists and foresters should direct their research programs toward more permanent methods of combatting insects.

Invariably too little is known of the biology and habits of the insect itself and the underlying causes that affect population fluctuations. Much can be learned in the laboratory, but field research in permanent plots and regional surveys are needed to complete the picture. Studies must be conducted not only in areas where outbreaks occur but — perhaps even more important — where they fail to develop; for in these latter areas may exist the clues to natural control — i.e., biological, climatic, tree and stand resistance, etc.

This information may then be translated into practical methods of control through silvicultural or forest-management practices.

And finally, every effort should be made to explore the possibility of practical control of insects by utilizing parasites, predators, and diseases; by developing strains of host trees resistant to insect attack; and eventually perhaps through irradiation.

## DISCUSSION

L. S. HAWBOLT. I should like to ask if greater successes have been obtained in planting seedlings under nurse crops of hardwoods, such as might follow fires.

R. C. BROWN. White pine weevil damage is much less severe to white pine when it is planted under a hardwood overstory.

W. J. CHAMBERLIN. (1) What is the cost per acre for protecting plantings with lead arsenate or DDT? (2) For what use are the *P. strobus* raised — Christmas trees? (3) Does DDT give protection for more than one season?

R. C. BROWN. (1) About \$4 per acre. (2) White pine is not used to any extent for Christmas trees in the Northeast. (3) Long-range protection depends on buildup following spraying and reinfestation from untreated areas. We are hoping for protection for 4 or 5 years.

F. P. KEEN. Are any figures available on the percentage of successful plantations in the U. S.?

R. C. BROWN. According to the Timber Resources Review recently released by the U. S. Forest Service, 76 per cent of the plantations in the United States are rated as successful. In the Northeast 63 per cent are rated successful.

R. R. LEJEUNE. In British Columbia Sitka spruce plantations on the lower mainland are so severely attacked by the Sitka spruce weevil that their future looks hopeless. On the other hand the thousands of acres of Douglas fir plantations have been free of insect pests to date.

# La Forêt du Portugal et ses Problèmes d'Entomologie Forestière

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## RESUME

En commençant par une appréciation des conditions écologiques du Portugal et de ces relations avec la végétation forestière "climax", l'auteur présente un court résumé des caractéristiques actuelles des forêts au Portugal continental, avec référence spéciale aux objectives de la sylviculture.

On arrive à conclure que la majorité des peuplements était à l'origine spontanée ou sous-spontanée, mais, actuellement, ils sont si modifiés par les techniques culturales qui peuvent être considérés comme des peuplements artificiels.

La partie de l'aire forestière occupée par les exotiques est relativement petite. *Eucalyptus globulus* (Labill.), est de loin l'espèce la plus importante.

L'auteur présente une liste des insectes nuisibles plus importants, rencontrés dans les forêts du Portugal continental et, un examen des conditions écologiques et culturales, en corrélation avec leur susceptibilité aux dégâts causés par ces espèces.

## INTRODUCTION

Dans ce travail j'ai prétendu établir la relation d'interdépendance qui peut exister entre le type actuel de la forêt portugaise et de la Sylviculture qui oriente son exploitation, sa résistance naturelle aux attaques des insectes nuisibles, et ses principaux problèmes d'Entomologie forestière, tout en me limitant, à peine, au territoire continental. Simplement il ne m'est pas possible d'aller au-delà de quelques exemples, correspondant notamment à la presque totalité des espèces économiquement les plus importantes.

J'ai cherché ainsi à présenter tout d'abord, et d'une manière résumée, les conditions écologiques qui caractérisent le milieu forestier portugais, ayant comme intention de faire ressortir les caractéristiques qui puissent avoir quelque rapport avec la résistance ou la susceptibilité à l'attaque des insectes nuisibles, en partant de l'idée fondamentale de l'immunité relative de la forêt climax.

Il s'agit donc d'une introduction à des études dans le sens pratique, d'une meilleure solution de ces problèmes, étant convaincu que la prophylaxie doit être l'objectif principal de l'activité de l'entomologiste forestier, chaque fois que les circonstances le permettent.

## LA FORET DU PORTUGAL

LE TERRITOIRE ET SON UTILISATION FORESTIÈRE: La superficie du Portugal continental est d'environ 8.900.000 ha.; elle se développe sur l'extrême sud-ouest de l'Europe, comme un long et étroit quadrilatère, orienté N-S, par 37° à 42° latitude N et 0° à 2° longitude E.

A l'heure actuelle on considère comme forestière une superficie correspondant à 30% du total: 2.670.000 ha., ainsi distribués:

"Montados" }	Pineraies .....	49%	(1.200.000 ha.)
	Chêneraies de liège .....	24%	(750.000 ha.)
	"      de chêne vert ....	13%	(350.000 ha.)
	Chêneraies d'autres .....	6%	(100.000 ha.)
	Châtaigneraies .....	5%	(80.000 ha.)
	Divers .....	2%	
		<hr/> 100%	

Les forêts de pins sont constituées en plus de 90% par *Pinus Pinaster*, et par *Pinus Pinea* presque exclusivement pour le reste. "Montados" c'est la désignation qui s'applique aux peuplements de chênes à feuilles persistantes, xérophiles: *Quercus Suber* et *Quercus Ilex*; les autres chêneraies, de "caducifolia", se composent de *Quercus Robur*, *Quercus pyrenaica* et *Quercus faginea*, comme dominantes. Aux bois de châtaigniers (*Castanea*

*sativa*) on donne le nom de "Soutos". Les bois divers se composent, pour la plupart, de plusieurs espèces d'*Eucalyptus* spp. (surtout *E. globulus*) et *Acacia* spp.

Les exigences de la défense du sol (combat contre l'érosion), de la mise en valeur des terrains pauvres, de l'assurance du pâturage sous-alpin (régime sylvo-pastoral), s'ajoutant à l'intérêt économique de l'augmentation du montant des matières premières forestières, conduisent à l'heure actuelle à considérer l'élargissement du patrimoine forestier jusqu'au taux de 40 à 50% comme nécessaire à l'utilisation rationnelle du territoire.

CONDITIONS PHYSIOGRAPHIQUES: On doit commencer par dire que, en ce qui concerne l'un quelconque des aspects élémentaires: sol, climat, végétation spontanée, comme pour ce qui a trait, en conséquence, aux aspects synthétiques, à une sumule écologique, les études portugaises n'ont pas encore atteint un détail et un ajustement nous permettant une représentation cartographique qui soit inattaquable en face de toute critique autorisée.

Du reste ce n'est pas là, on le sait, une situation exclusive.

*Hypsométrie*: C'est le plus grand fleuve, le Tage, qui fait la principale division du pays; 58% du territoire, de caractéristiques montagneuses, s'étend au nord de ce fleuve; 42% au sud, avec des caractéristiques opposées, sousplaines. En effet, du point de vue hypsométrique l'on peut résumer:

Dans la zone sous-alpine:

0,51% du territoire (totalement au nord du Tage)

de 1400 à 2000 m..... 0,14%

de 1200 à 1400 m..... 0,37%

Dans la zone moyenne:

77,70% du territoire:

de 200 à 400 m..... 28,36%

de 50 à 200 m..... 31,33%

Dans la zone basse: (moins de 50 m.)

11,79% du territoire

de 700 à 1200 m..... 11,02%, seulement 0,8% au sud du Tage

de 400 à 700 m..... 17,01%, seulement 7,5% au sud du Tage

On retient, comme première conclusion, que la très grande partie du territoire au-dessus de 400 m. demeure au nord du Tage.

*Carte des sols — conditions agrologiques*: Les pédologues portugais sont d'accord pour attribuer à ce pays, en matière de classification des sols, non pas une dominance zonale mais plutôt celle des circonstances azonales et intrazonales. On admet que les 60% du territoire doivent leurs caractéristiques à la nature du matériel originel (roche mère). Rien d'avantageux en résulte du point de vue agrologique et de la culture.

En résumé, les conditions géologiques se présentent comme suit:

terrains anciens	67%	{ 33% paléozoïques
		{ 25% granits
		{ 9% autres
" mésozoïques	10%	
" cénozoïques	23%	

et cela revient à dire que les ressources, pour la fertilité, sont plutôt faibles, partant de conditions naturelles pauvres ou manquant d'équilibre. Le très fort relief des régions au nord du Tage vient ajouter fréquemment aux inconvénients dus à la roche-mère ceux de l'inclinaison des escarpes. Voilà pourquoi les types de litosols ou sols squelettiques et leurs voisins les sols litoliques ou sous-squelettiques sont signalés dans notre carte des sols constamment. L'expansion de la culture, phénomène naturel dans un pays où l'accroissement de la population est, lui-même, fort accentué, se montre aussi responsable du dépérissement du sol, en provoquant souvent des traces d'érosion.

Pour ce qui est de l'influence pédogénique du climat il faut se rendre compte de la façon alternante, du type méditerranéen, avec laquelle opère le régime pluviométrique

question importante du point de vue lessivage; à une saison humide (semestre été-automne) les pluies les plus fortes sont coincidentes avec les plus basses températures; les mois les plus chauds sont secs ou presque, et l'on sait bien ce que cela signifie pour la végétation.

Du fait de cette extension de la culture agricole on ne trouve chez nous que d'une façon limitée le sol naturel du pédologue, celui-ci rencontre constamment des types intermédiaires ou mal définis, incapables de se classer dans une classification pédologique plutôt rigide. Tout de même il est toujours possible de distinguer deux grandes influences: celle du climat pluvieux du nord-ouest et des hautes montagnes, dont l'orientation consent l'action maritime plus ou moins lointaine, et celle du climat plutôt sec du sud, plus typiquement méditerranéen ou même continental-ibérique. Une forte couverture de végétation ligneuse, d'arbres et d'arbustes, a dû réaliser sous cette première influence une action sur le sol qui se traduit par des procédés de podzolisation plus ou moins avancée; et encore à l'heure actuelle cette action se poursuit en des parcelles du territoire. Au contraire, vers le sud, en régime pluviométrique opposé, quelquefois les mêmes conditions de roche-mère, par manque de couverture abondante, sont passibles de présider à la formation de sols bien différents. On rencontre des podzols, des sables podzolisés et des sables podzolisés sur "arenitos",<sup>1</sup> surtout au littoral du Nord avec occupation par les pineraies. Les sols bruns podzoliques — sols bruns forestiers — avec les litosols et sols litoliques correspondants s'étendent à travers toute la région montagneuse du nord du pays.

Sur le territoire mésozoïque, qui s'étend dans le centre littoral, entre les parallèles 38°65 et 39°40, on signale des sols rouges (méditerranéen) de calcaires et aussi des sols bruns de calcaires.

Vers le sud du Tage des terres brunes (sans calcaires) ou la pluviosité est moindre; ce sont les sols de l'Alentejo intérieur; là se trouvent les plus grandes extensions céréalières, avec aussi des sols rouges (méditerranéens) non calcaires, un peu plus fertiles. Des terres de blé assez riches s'y mélangent "Barros pretos" — argiles noires — mais, malheureusement, dans une proportion minime. Vers le littoral, et en suivant le grand fleuve Tage et ses affluents, à part les terrains alluvionnaires de productivité traditionnelle, de formations très étendues du cénozoïque ont trouvé avec la domination de "arenitos".

Vers l'extrême intérieur les conditions climatiques deviennent plus rigoureuses, et les terrains plus compacts.

Pour l'extrême sud, dans l'Algarve, les conditions pédologiques deviennent plutôt mélangées, mais le climat très sec limite de beaucoup les effets d'une richesse potentielle qu'on aimerait trouver ailleurs.

*Conditions du climat:* Pour la définition des principaux types climatiques il est nécessaire de faire place à l'influence de la littoralité et de la continentalité, contraire, et à celle très marquée de l'altitude. L'action adoucissante du voisinage de l'Océan Atlantique est décisive, d'autant plus qu'une branche du Courant du Golfe dont l'inflexion se fait sur la côte portugaise par 39° de latitude, en ajoute les effets. Cette dernière influence est si marquée que certains écologistes, comme le Prof. Emburger, attribuent au Portugal plutôt un climat méditerranéen un peu partout. En réalité le "faciès" atlantique-nord pur n'est présent que dans l'angle nord-ouest ou à peu près. Ce qui existe c'est un mixte d'influences s'affirmant continuellement et c'est ce que révèle la carte écologique esquissée par le Service de l'Etat employant à tout propos les notations AM et MA (signifiant: climat méditerranéen). Sur les montagnes le climat est désigné oro-atlantique vers les 1200 m. et au-dessus, et cela chaque fois que l'influence maritime est enregistrable; à l'étage inférieur le climat est sous-atlantique ou mélangé avec M (méditerranéen). Le même type M domine au sud du Tage. Mais à mesure que la continentalité progresse c'est le type ibérique (I) qui s'affirme; on l'atteint dans le voisinage de l'Espagne et aussi, du reste, vers l'extrême Nord-Est du pays, là où la disposition des reliefs empêche l'influence océanique de s'exercer, et le climat de la "Meseta Iberica", excessif, à étés et hivers rigoureux et pluies inférieures à 1000 m., se développe en toute puissance.

<sup>1</sup> Roche sablonneuse — grès.



Pour ce qui regarde l' "Algarve", tout au sud, quoique typiquement méditerranéen, il offre deux aspects: celui du dessus du vent ("barlavento") et celui du dessous du vent ("sotavento"); le premier est plutôt sous-méditerranéen ou atlantique-méditerranéen, le second euméditerranéen. Encore, dans le premier cas, une certaine influence du large macaronaisique, peut elle être enregistrée.

QUELQUES INDICES ÉCOLOGIQUES: On peut ajouter sous ce rapport quelques informations complémentaires. Une "*sylva climatica*", du reste peu abondante en essences, mais suffisamment expressive, est capable en égard à la conception basique du "climax" de prêter aide à la caractérisation du territoire. La circonstance, citée auparavant, de l'expansion culturelle démesurée qui a mené, un peu partout, à la destruction de la couverture naturelle ou spontanée, explique que très souvent on ne rencontre aujourd'hui que des vestiges de cette "*sylva primitiva*".

Ces vestiges précieux se trouvent, comme d'habitude, dans les régions moins habitées, en pleine montagne, quoique ici encore les abus du pâturage aient fait leur rôle destructeur. Tel qu'on l'a dit, la liste des espèces fondamentales susceptibles de caractériser notre "*sylva climatica*" n'est pas grande; il est intéressant d'y placer en premier lieu, et presque avec exclusivité, le genre *Quercus* et une petite demi-douzaine d'espèces lui appartenant. C'est d'abord le *Quercus Robur* des régions pluvieuses et pour un climat plutôt atlantique; sous une latitude pareille, se suit à l'intérieur et vers les hauteurs dans certaines limites, le chêne de la montagne, *Quercus pyrenaica* dans la région ibéro-méditerranéenne. Pour la situation centrale du pays, méditerranéenne-atlantique, la représentation revient à *Quercus faginea*, dont le polymorphisme foliaire est grandement accentué; l'adaptation de l'espèce à cette caractéristique, plutôt intermédiaire, interférente, atlantique-méditerranéenne, de notre climat, est si remarquable que la désignation de *chêne portugais* lui revient par l'usage déjà ancien, quoique l'espèce *Quercus lusitanica*, modeste, frutiqueuse, soit une toute autre plante de chez nous. Pour le reste, région méditerranéenne, on trouve *Quercus Suber* surtout près du Tage terminal et dans le littoral-sud cependant se trouve dispersé partout, à l'exception des zones de climat ibérique, où c'est alors l'occasion de *Quercus Ilex* de devenir l'indice climacique.

Quand on se souvient de l'importance relative du recouvrement forestier actuel pour les diverses espèces, on peut s'étonner de n'avoir pas encore trouvé une référence quelconque aux pineraies et à l'espèce *Pinus Pinaster* (occupant les 50% de la superficie) pour ce qui regarde cet aperçu écologique. C'est que l'introduction de l'espèce est récente et, au point de vue écologique, il ne lui appartient pas de figurer à côté des chênes et des chêneraies. Cette introduction revient quand même à quelque 8 siècles et a été faite avec du matériel d'origine française. L'espèce a trouvé en son habitat nouveau des conditions si favorables et s'est montrée si utile qu'une large et prompt expansion s'en est suivie et continue aujourd'hui encore. Elle occupe surtout le littoral sablonneux et, en des superficies importantes, l'ancienneté du peuplement a dû conditionner une certaine action pédogénique (processus de podzolisation) et aussi un état para-climacique doit, paraît-il, être atteint plusieurs fois; mais c'est tout ce qu'on peut avancer pour ce qui concerne ce type de végétation.

On peut dire de même à propos des peuplements de châtaigniers (*Castanea sativa*); l'introduction de l'espèce, quoique plus reculée, est considérée certaine et pour la définition écologique moins valable, donc, la présence des châtaigneraies de chez nous.

En dehors, cependant, des espèces silvicoles de catégories supérieures suscitées, une espèce de l'arboriculture, plutôt extensive, est fondamentale comme indice écologique: c'est l'olivier (*Olea europea*  $\beta$  *sativa*) et plutôt encore la variété spontanée, très rustique, *Olea europea*,  $\alpha$  *Oleaster* ("zambujeiro" — olivier sauvage). On peut dire que le climat méditerranéen s'attache, comme définition, à l'existence de cette espèce qui se trouve avoir la qualité d'unité climacique fondamentale.

L'extrême Sud (l'Algarve) trouve une assez bonne représentation écologique en *Ceratonia Siliqua* (caroubier). Les hautes montagnes du Nord, à leur tour, trouvent en des espèces de *Betula*, comme *Betula celtiberica*, un indice de "*sylva climatica*".

VÉGÉTATION SPONTANÉE — INDICES DE DÉGRADATION: Puisque le *Quercetum*, quoique spécifiquement variable par accord avec les conditions climo-édafiques particu-

lières, est le type climacique de la végétation qui aurait dû (on l'a déjà vu) recouvrir la plus grande partie du territoire, les associations floristiques véritables chez nous devraient s'intégrer, de leur côté, à ce type poli-spécifique, et auraient tâche de compléter la couverture du sol avec stabilisation et conservations assurées. Malheureusement, ce n'est pas là le spectacle qui se déroule devant les yeux du phytosociologue au Portugal, à moins d'une réserve sur des parties limitées du territoire. La raison en est dans des motifs déjà entrevus, le principal étant l'intromission de la culture et l'espèce de désarticulation qui en est advenue sur le climax primitif.

D'après mes objectifs, en rédigeant cette communication, il se suivrait, si le temps le permettait, une documentation sur la question qui possède la valeur économique la plus forte, c'est-à-dire pour les superficies recouvertes par les pineraies et les "montados" de chêne-liège, et de chêne-vert. Il y a lieu de dire seulement que pour ces deux types de peuplements et surtout pour le second, les études phytosociologiques, en voie de grand progrès chez nous, révèlent fréquemment des conditions d'équilibre plutôt instable et que, plusieurs fois, c'est le cadre de la grande dégradation qui se fait voir, qui peut être représenté par des indices propres.

**SYLVICULTURE:** Si maintenant on prête attention aux conditions qui président au Portugal à la création et à la conduction technique des peuplements forestiers, d'autres éléments peuvent encore s'ajouter qui nous aident à faire lumière sur les fondements, ou la raison lointaine, de quelques-uns de leurs problèmes entomologiques les plus importants.

Distinguons d'abord les peuplements d'origine spontanée (climacique) de ceux qui, quoique constitués par des espèces introduites il y a longtemps, doivent encore être considérés d'origine artificielle, ou plutôt sous-spontanée (en raison de l'antiquité de l'introduction); ensuite il va falloir considérer les peuplements formés par des exotiques d'une introduction récente.

En premier lieu ce sont les cas des "montados" de chêne-liège et de chêne-vert et des autres chêneraies. De ce qu'on peut concevoir comme ayant été le *Quercetum Suberis* on est parvenu à une espèce de forêt-verger ("floresta-pomar"), en raison de la destruction presque totale de la végétation spontanée du sous-bois et de la couverture vivante moindre et en raison, aussi, de la réduction des arbres du peuplement tombant très bas. L'agriculture et le pâturage, co-associés à la sylviculture, font revêtir les peuplements d'un faciès franchement artificiel. Du fait de la participation agricole, les mobilisations périodiques du sol, l'incorporation de fumures et d'autres fertilisants, deviennent des pratiques usuelles. Périodiquement aussi les arbres sont taillés et élagués et quoique ces opérations soient règlementées, bien des fois elles échappent à toute fiscalisation et les abus se succèdent avec des conséquences physiologiquement néfastes. Les éclaircies ("desbastes"), quoique également règlementées, le pâturage des pourceaux se nourrissant de glands et les incendies, de leur côté, contribuent à une faible régénération naturelle: et ce qui lui manque est très rarement compensé. Comme conséquence, les forêts de chêne-liège au Portugal sont pour la plupart des peuplements pures et équiennes, d'une faible densité, aux prises contre des actions contraires à l'immunité naturelle, parmi lesquelles il faut encore citer l'extraction du liège, elle-même, un mal nécessaire, qui à la longue, étant une opération anti-physiologique, apporte à la résistance des individus un affaiblissement plus ou moins marqué, d'ordre général. Une moindre résistance aux insectes nuisibles en est une des modalités immédiates.

Il y a lieu de faire des considérations semblables pour ce qui regarde les "montados" de chêne-vert d'autant plus que le *Quercetum Ilicis* se développe en des conditions de milieu parfois assez difficiles. Il ne s'applique seulement à ce qui a trait à l'extraction de l'écorce, laquelle — comme on le sait — n'est pas pratiquée.

Dans les autres chêneraies l'artificialisme de la culture est bien mineur; on peut dire qu'elles se maintiennent assez près de leur structure climacique, sans intervention agricole ou du pâturage.

Dans le groupe des peuplements forestiers formé par des exotiques introduits depuis plusieurs siècles nous englobons les châtaigneraies et les pineraies (de *Pinus pinaster*).

Les premiers ont été de tout temps conduits comme des peuplements artificiels, tant pour la production du fruit et du bois — s'avoisinant par la structure de celle des vergers — comme pour la production exclusive du bois, ordinairement exploitée en taillis et constituant dans ce cas un type bien défini de forêt artificielle. C'est à cause de l'expansion de la "maladie de l'encre" qu'une transformation dans ces peuplements est depuis longtemps en train de s'opérer par l'élimination progressive des individus. Ici, encore, l'agriculture et le pâturage co-associés, ont pu exercer une fâcheuse influence sur les conditions de résistance, en raison de la destruction de la végétation spontanée. Les peuplements sont d'habitude équiennes également.

En ce qui concerne les pineraies, d'une si grande importance (rappelons toujours qu'elles recouvrent 50% de la superficie forestière) il existe aussi un panorama fort critiquable à mon point de vue. Tout de même il faut distinguer ce qui appartient à l'Etat, dans les landes littorales et dans les montagnes plus ou moins intérieures, de ce qui revient à la propriété privée. La distinction s'impose dès lors à partir du procédé de l'exploitation: chez les pineraies de l'Etat on voit suivre des règles techniques et un plan d'aménagement; chez les autres il n'existe pratiquement aucune règle scientifique, aucune orientation ayant trait à l'Economie forestière.

Les pineraies de l'Etat sont pour la plupart des peuplements pures et équiennes, exploitées à blanc étoc; celles des particuliers se présentent irrégulières, à âges multiples et exploitées en jardinage. Chez les premières on opère les éclaircies réglementaires, tandis que dans les secondes on n'observe pas un critérium technique et c'est plutôt l'intérêt immédiat du propriétaire qui se présente, au dehors de l'intelligence technique du problème. Et la conclusion est que, de cette façon, les conditions de l'auto-résistance ne sont pas défendues. On doit faire référence à la suppression fâcheuse de la couverture vivante, de remplissement, et pire que cela, parfois, la propre couverture morte, la litière s'en va, avec appauvrissement du sol de la forêt.

Il faut encore signaler que l'introduction de la culture du *Pinus pinaster* en des emplacements ou stations moins favorables, par hauteur excessive ou exposition non maritime, est susceptible de diminuer la résistance de l'espèce et l'état dans lequel se trouvent certains peuplements en est la preuve.

Et il n'existe pas encore au Portugal des efforts sérieux dans le sens de l'introduction de variétés ou de races plus résistantes aux attaques des insectes.

Parmi les exotiques d'une introduction plutôt récente (une centaine d'années ou moins) l'unique place mentionnable appartient au genre *Eucalyptus* et aux espèces *E. globulus*, dominante, et *E. camaldulensis*, celle-ci très limitée. D'ordinaire l'exploitation en est faite en taillis et les peuplements, dans la grande majorité sont très denses, n'ayant pas de sous-bois. Toutes les autres exotiques, et il y en a plusieurs, tout aussi bien parmi les résineuses que parmi les feuillues, n'occupent actuellement encore que des superficies insignifiantes et cet aperçu général n'a pas raison de s'en occuper.

En résumé on peut conclure que du fait de ce qu'il appartient aux propriétaires privés la presque totalité du territoire forestier portugais (90% au moins), se régissant par des procédés hors des règles techniques et sous l'influence agricole courante, et cela malgré l'excellence des Services Forestiers de l'Etat et des efforts qu'ils révèlent dans le sens de l'amélioration et du progrès.

Mais ce qu'il convient de retenir, pour le moment, quand il s'agit de définir les conditions du problème de la résistance aux insectes nuisibles, c'est que les modalités de la culture forestière à l'heure actuelle ont comme dominant l'aspect défavorable du point de vue auto-défense des peuplements.

La lutte contre les fléaux forestiers au Portugal, insuffisante comme l'est, en conséquence, sa prophylaxie réalisée par la sylviculture, a été dernièrement basée dans l'emploi d'insecticides, surtout les organiques synthétiques (D.D.T. et B.H.C.), emploi qui en certains cas a été fait d'une manière généralisée, avec recours en quelques exemples à l'avion. Etant donnés les inconvénients déjà reconnus en certains cas d'un tel procédé, on croit aussi devoir signaler cette circonstance dans le sens de l'influence indirecte qu'elle peut exercer dans l'importance économique de certaines espèces d'insectes qui constituent quelques-uns des plus graves problèmes de l'Entomologie forestière portugaise.

## LES PRINCIPAUX PROBLEMES D'ENTOMOLOGIE FORESTIERE

Après avoir présenté, jusqu'ici, un aperçu général des conditions mésologiques de la forêt portugaise et de l'orientation selon laquelle celle-ci est menée, il s'agit maintenant, en terminant, d'établir les relations entre cet aperçu et les problèmes que présente au Portugal l'Entomologie forestière pour ce qui y va de plus important.

"MONTADOS" DE CHÊNE-LIÈGE: Les principaux insectes nuisibles sont: *Lymantria dispar* (Lepidoptera-Lymantriidae); *Tortrix viridana* (Lepidoptera-Tortricidae); *Aperichlista* sp. (Hymenoptera-Tenthredinidae); *Coroebus undatus* (Coleoptera-Buprestidae); *Coroebus fasciatus* (Coleoptera-Buprestidae); *Cremastogaster scutellaris* (Hymenoptera-Formicidae); *Cerambyx cerdo* (Coleoptera-Cerambycidae).

En vue de ces relations nous trouvons pleinement justifiée par la structure artificielle des peuplements la présence de *Lymantria dispar* et son élargissement dans une vaste superficie; mais plusieurs fois on ne trouve au contraire une prompte justification à des attaques d'une proportion toute autre, assez modestes, sauf en certains cas où l'on en enregistre la présence, à une certaine échelle, de la végétation du sous-bois ou bien une plus grande densité d'arbres. Comme il s'agit, en effet, d'un insecte préférant les peuplements ouverts, avec un micro-climat intérieur sec et chaud, précisément les "montados" dépourvus de sous-bois et à une densité faible lui offrent, partout où sont favorables les conditions mésologiques, générales les meilleures opportunités pour son développement.

La présence généralisée en des régions diverses du *Coroebus undatus* peut se relationner aussi avec le mauvais développement des "montados" attaqués, surtout là où les conditions agrologiques sont moins favorables.

Pour ce qui regarde les autres espèces il n'y a que *Cerambyx cerdo* qui puisse, moyennant les connaissances actuelles, dénoncer quelque relation avec la Subériculture, une fois que la présence de l'insecte et son abondance sont corrélacionnées avec l'existence de blessures résultantes d'une taille exagérée, d'un écorcement mal fait ou bien d'accidents qui lui sont survenus, ou encore de la présence d'arbres morts ou tout simplement caducs. Ils sont très rares les "montados" où l'on n'observe, plus ou moins, des individus en ces conditions, quoique leur nombre soit réduit à partir d'une exploitation bien orientée plutôt rare.

La présence maintenant assez répandue, au sud du Tage, d'un insecte nocif encore mal identifié *Aperichlista* sp. (?), on peut la relationner avec les traitements faits à base de D.D.T. sur l'aire aujourd'hui attaquée où *Lymantria dispar* a été presque totalement contrôlé. Faute d'études qui aient été réalisées dans le sens d'élucider l'interdépendance des deux faits, on ne peut donner une affirmation concrète; seule la suspicion est de tout point légitime vu que l'invasion de cet insecte n'avait jamais été signalée avant que les traitements eussent lieu et aujourd'hui, au contraire, les dégâts sont notoires. Egalement il semble légitime d'établir interdépendance envers *Lymantria dispar* et *Tortrix viridana* (le combat de la première permettant l'invasion de la seconde), du moins à partir d'un exemple concret.

"MONTADOS" DE CHÊNE-VERT: Les insectes nuisibles plus importants sont: *Tortrix viridana* (Lepidoptera-Tortricidae); *Malacosoma neustria* (Lepidoptera-Lasiocampidae).

Pour l'un quelconque de ces deux cas des relations de cause à effet, relativement à la structure des peuplements et à la culture respective, d'une part, et d'autre part au processus entomologique, ne peuvent pas être établies. La première, d'abord, est un insecte endémique, comme de tout temps, qui souffre de fortes oscillations en ce qui concerne l'intensité des attaques en raison, on le croit, des variations périodiques du climat local.

La *Malacosoma neustria*, au contraire, appela sur elle récemment les attentions en raison de dégâts importants sur une vaste surface en partant de la frontière espagnole. Comme il s'agit d'une espèce de la faune portugaise connue il y a longtemps, le fait qu'aucune invasion notable n'ait été dénoncée auparavant, en présence des attaques actuelles, constituant une nouveauté, se montre d'une interprétation difficile; toutefois on accepte que la Sylviculture, cette fois, n'en soit encore en aucune façon responsable.



AUTRES CHÊNERAIES (DE "CADUCIFOLIA") : On n'enregistre point d'insectes nocifs importants; très rarement les présences constatées s'élargissent de façon à devenir économiquement valables; et si quelquefois des exceptions tout à fait locales se produisent, les raisons en restent inexpliquées. A leur relative intégrité, au point de vue phytosociologique, s'attribue en grande partie sa résistance aux attaques des insectes nuisibles.

CHÂTAIGNERAIES : Leurs insectes nuisibles sont : *Euproctis chrysorrhoea* (Lepidoptera-Lymantriidae); *Phalera bucephala* (Lepidoptera-Notodontidae).

Le premier a été enregistré, la première fois, il y a 50 ans, en diverses localités comme ayant acquis une grande importance économique; dès lors des attaques sérieuses n'ont pas été signalées, quoique toujours présent. Toutefois, et cela de même avec l'autre espèce, toute raison qui puisse satisfaire l'interprétation de leur actualité nous échappe.

PINERAIES (PINUS PINASTER) : Les insectes nuisibles importants sont : *Thaumetopoea pityocampa* (Lepidoptera-Thaumetopoeidae); *Pissodes notatus* (Coleoptera-Curculionidae); *Myelophilus piniperda* (Coleoptera-Ipidae); *Ips erosus* (Coleoptera-Ipidae); *Ips sexdentatus* (Coleoptera-Ipidae).

C'est la première de ces espèces qui est la plus répandue et celle qui cause de plus grands dégâts; on peut dire que sa présence dans les peuplements est l'indice des conditions mauvaises mésologiques dans lesquelles se trouvent ces derniers. Ainsi, dans la région littorale où se trouve la plus grande forêt de l'Etat "Pinhal de Leiria", considérée station optimum pour l'espèce, cet insecte n'est que très rare; cependant vers l'intérieur et en montagne dans des expositions tranmontaines, les attaques peuvent atteindre de fortes proportions. Ici du moins, la Sylviculture est alors responsable quand elle choisit des emplacements mésologiquement inconvenables. On observe le même en regard du *Pissodes notatus*, toutefois à une échelle moindre, vu que l'invasion se fait en des conditions circonscrites.

Les trois autres espèces citées s'attaquent surtout aux peuplements affaiblis, comme c'est la règle pour plusieurs espèces d'Ipides; et en conséquence il est assez facile d'établir des relations de dépendance avec un manque d'orientation technique dans la conduite de ces peuplements, ou bien avec une culture par des méthodes impropres. Ils sont tous assez vulgaires, mais d'habitude ne correspondent pas à de fortes invasions; une exception pour *Ips sexdentatus* doit se placer en regard à l'attaque survenue après le cyclone du 15 février 1941 qui assola le Pays. En cette occasion, l'aire couverte et l'intensité de l'invasion originèrent des dégâts exceptionnels parce que l'élimination des déchets de toute sorte n'a pas été faite à temps et en conséquence les insectes ont trouvé des conditions tout à fait propices à son développement.

EUCALYPTUS (SPP.) : En ce qui concerne les peuplements d'*Eucalyptus* spp., jusqu'ici ils se sont montrés exceptionnellement résistants aux insectes; aucun de leurs ennemis originaires n'a été introduit, ni aucun des éléments de l'entomofaune autochtone n'a démontré une capacité d'adaptation aux espèces cultivées, en des termes sérieux. Le cas le plus noté fut celui enregistré en 1924 en des plantations récentes de *E. globulus* attaqués par les larves de *Melolontha papposa* var. *hybrida* (Coleoptera-Scarabaeidae).

Ce qu'il faut précisément signaler c'est cette invulnérabilité des *Eucalyptus* spp. chez nous, d'autant plus que dans la voisine Espagne et surtout au Nord de l'Afrique quelques insectes nuisibles ont été notés et jamais en conditions identiques au Portugal.

## CONCLUSION

Le Portugal n'a pas actuellement, dans la partie de son territoire auquel j'ai restreint mon exposition, des forêts en condition de maintenir l'immunité propre des formations climaciques excepté les chêneraies en certains cas; la Sylviculture, quelle que soit son orientation, s'étant emparée de l'exploitation de tous les peuplements existants, tant d'origine spontanée que sous-spontanée ou exotique, il en résulte qu'elle est la principale conditionnatrice, de l'état de vitalité de ceux-ci.

Les conditions mésologiques, quoiqu'elles soient, sous certains aspects, notamment les pédologiques, manifestement défavorables à un bon état de vitalité de la forêt



portugaise, ne peuvent être considérées de nature tellement ingrate qui justifie, par elles seules le développement des insectes nuisibles au point de constituer de graves problèmes économiques.

Le climat, d'aménité relative, s'il favorise cette vitalité contribue par ailleurs de forme identique au développement de ces insectes, sans toutefois, sauf dans des cas exceptionnels, pouvoir être également considéré comme la cause lointaine fondamentale de la relative susceptibilité de ces peuplements à leur attaque.

Il semble donc qu'on puisse conclure de l'appréciation du cas portugais d'Entomologie forestière que le facteur le plus important à un tel point de vue, consiste dans l'état plus ou moins avancé de la déprédation des forêts spontanées et dans l'excès d'artificialisme de la constitution actuelle des forêts d'origine sous-spontanée ou exotique, cela comme conséquence d'une sylviculture imparfaite dans le sens de l'action prophylactique qu'elle doit exercer lorsque basée sur une convenable orientation technique.

#### DISCUSSION

W. J. CHAMBERLIN. Do all the species of *Quercus* produce commercial cork?

C. M. BAETA NEVES. Only the cork oak produces commercial cork; Portugal is the first producer of cork in the world. The other oaks produce a small quantity of cork for tanning.



# Problems Caused by Insects in Lake States Forest Plantations

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## ABSTRACT

*Pine plantations, predominantly Pinus resinosa and P. banksiana, were established on vast areas of cutover and burned land between 1932 and 1938. These plantations, added to those previously established, created continuous pine forests of similar age class on both State and National Forests.*

*Insect problems immediately presented themselves and have been on the increase with the passing of time. First was damage to the newly planted trees by white grubs, members for the most part of the genus Phyllophaga. The abundance of these insects was directly related to the proximity of suitable food plants for the adult beetles, especially birches, poplars, and oaks. Their injury to the roots was all the more severe due to a series of unusually dry seasons between 1932 and 1936.*

*Following the injury by white grubs other pests appeared, some that had seldom been observed prior to the establishment of extensive contagious stands of the same age. Other well known species became more numerous, some exhibiting changes in their habits. Among these the Saratoga spittle bug, Aphrophora saratogensis, became especially numerous and injurious in plantations growing on certain soil types; and some defoliators caused and are causing severe local damage from time to time.*

*In this paper the sequence of species both old and new is discussed from the ecological viewpoint.*

## INTRODUCTION

The history of the forest lands of the Lake States has been one of extremes. Beginning with logging of the virgin pines, haste has been the controlling influence in forest practice. The inexpensive building materials provided by the pineries of Michigan, Wisconsin, and Minnesota made possible the rapid settlement of the rich prairie lands of the Central States. It was natural, therefore, that rapid and wasteful exploitation should have characterized logging operations when the demand for wood was great and the forest was apparently inexhaustible.

As the pines were cut, the lands, once forested, were burned and reburned, often intentionally, to keep them open for prospective agricultural occupancy. By the time it was recognized that most of the lands originally occupied by pine forests were not suited to agricultural use, thousands of square miles had been devastated, and before they could again be made productive, planting was necessary.

Again extreme measures prevailed. As the planting program grew in momentum it was given such emphasis that reforestation in the minds of many became synonymous with forestry and strenuous efforts were made to reclothe the vacant acres with trees as rapidly as possible. No thought was given to consequences of too much of the same species and age class on contiguous areas. Otherwise insect problems which we face today could have been foreseen and, in part at least, avoided.

The infestations of insects, begotten by the undue haste that prevented careful planning, now constitute serious threats to the pine plantations. Emergencies calling for prompt action are frequent. Again, apparent pressure for time has fostered the extreme viewpoint. Far too much reliance is being placed on the effectiveness of insecticidal treatments, because they are direct and easily understood, and too little to the possibilities of controlling insects by less spectacular silvicultural practices. As a result, wide-spread spraying programs are often entered into without much thought of either the ecological or economic implications.

A full tree generation will probably be required before a balanced viewpoint toward the management of planted forest lands in the Lake States can be attained. In the meantime, excessive injury by insects may be expected.

The extensive areas of single species forests, in approximately the same age class, that resulted from the very intensive planting program during the decade between 1930 and 1940, have suffered severely from insects. Many of the insects concerned were never before numerous enough to cause serious injury, and old pests have adopted new habits and have appeared in large numbers under unexpected situations.

For example, the white pine weevil, *Pissodes strobi* (Peck), once restricted as a pest to white pine, *Pinus strobus* (L.), Norway spruce, *Picea abies* (L.), and to a lesser degree to Scots pine, *Pinus sylvestris* (L.), is adapting itself to red pine, *Pinus resinosa* (Ait). The Saratoga spittle bug, *Aphrophora saratogensis* (Fitch), known only in museum collections in 1940, is today one of our most serious pests of sapling hard pines. A number of tip and shoot moths, formerly considered innocuous, especially members of the genera *Petrova*, *Dioryctria*, and *Eucosma*, are common and sometimes highly injurious in pine plantations. Sawflies of the genera *Diprion* and *Neodiprion* are especially serious defoliators of pine plantations. Several defoliators introduced from Europe, *Neodiprion sertifer* (Geoff.) and *Rhyacionia buoliana* (Schiff.) have increased their range and seriousness as pests. The so-called anomala beetle of jack pine, *Anomala oblivia* (Horn), was practically unknown until 1935, when it became numerous in lower Michigan jack pine.

Still other pests that have recently become excessively numerous in plantations might be mentioned but those referred to will serve to illustrate the increased incidence of certain pests that has been associated with the establishment of young pines on extensive and contiguous areas. But these new pests are by no means the only insects injurious to planted pines, and in this paper we shall consider a group of these older pests.

### CHAFER GRUBS IN FOREST PLANTATIONS

Among the old pests of newly planted trees are the white grubs, larvae of chafer beetles. During the peak of planting activities during the decade, between 1930 and 1940, the injury caused by these insects was especially severe.

Beginning in 1934 and continuing through 1937 a cooperative study of these insects was conducted in the Lake States. It included the following organizations: The U.S. Forest Service, the then Bureau of Entomology and Plant Quarantine, U.S.D.A., the Civilian Conservation Corps, which provided substantial financial support and man power, the Conservation Departments of the three states, the University of Minnesota, and University of Michigan. The study of chemical treatments was conducted chiefly by members of the University of Minnesota staff; and direction of ecological studies and a region wide survey of conditions were the responsibility of the University of Michigan and the Bureau of Entomology and Plant Quarantine. After Civilian Conservation Corps appropriations ceased to be available, the project was continued intensively for one season with funds allotted from the Faculty Research Fund of the University of Michigan.

Since then ten 40-acre plots established in 1936 have been under intermittent observation. These were established to study natural vegetational changes that occur over a considerable number of years, and to study the influence of these changes upon the food plants of adult chafer beetles. These plots will be re-examined in detail in 1957, after which the complete results of the grub investigations will be prepared for publication. In the meantime, it may be of interest to present tentative conclusions that have been derived from a partial analysis of the data.

During 1934 a superficial examination of newly established pine plantations was made throughout the Lake States. This disclosed that severe grub damage was common. The damage was not uniformly distributed. In some plantations losses were excessive whereas others suffered only slightly or not at all. These observations led to the suspicion that the amount of injury might be related to recognizable local conditions, most likely types of plant cover.

With this thought in mind, a general survey was made of the beetle species present, the grub population numbers, the character of the vegetation and the seedling mortality in all plantations near Civilian Conservation Corps Camps in the Lake States. Almost every publicly owned pine plantation which had been established

Information concerning the plantations was collected on one-tenth-acre plots spaced approximately 5 chains apart along lines following the direction of the planted rows of seedlings. An attempt was made to locate each plot in a spot where the vegetation was uniform as to plant species, distribution, and density. Therefore, if a plot fell by measurement at a point where a type change occurred, its position was shifted slightly so that it would lie entirely within one type or the other.

Simultaneously with these extensive studies, more intensive work was conducted in Michigan. Food preferences of adults and larvae were observed and information on the life cycles and the economic status of a number of grub species was obtained. The knowledge thus gained has been helpful in interpreting the more extensive observations. Intensive work in the Upper Peninsula of Michigan was conducted by J. R. Gross and in the Lower Peninsula by L. E. Yeager, both under supervision of the author. Yeager's doctoral dissertation was based upon his intensive studies, and has been drawn upon freely in the preparation of this paper.

Fourteen of the twenty-nine species of *Phyllophaga* recorded from the Lake States were observed during our investigations (Table I). The others are for the most part

	1	2	3	4	5	6	7	
Approx. no. collected	3900	1000	1700		650	1600	100	
<i>Phyllophaga</i>								
<i>drakei</i> (Kirby)	x	x	x	x	x	x	x	Abundant
<i>gracilis</i> (Burmeister)	x				x	x	x	Local
<i>marginalis</i> (LeConte)	x	x			:	x		Common
<i>anxia</i> (LeConte)	x	x	x	x	x	x	x	Abundant
<i>rugosa</i> (Melsheimer)	s x				x	x	x	Rare north
<i>rubingosa</i> (LeConte)	x					x	x	Scarce
<i>prunina</i> (LeConte)	x						x	Scarce
<i>ilicis</i> (Knoch)	s x			s x			s x	Rare
<i>micans</i> (Knoch)	x							Rare
<i>tristis</i> (Fab.)	s x						s x	Rare
<i>fusca</i> (Froelich)		x			x		x	Rare
<i>barda</i> (Horn)		s x					x	Rare
<i>crenulata</i> (Froelich)	s x			s x			s x	Common
<i>futilis</i> (LeConte)		x		x				Scarce

1. Huron Nat. Forest
2. Marquette Nat. Forest
3. W. Upper Mich. & N. Wis.
4. Minnesota Forests
5. E. Upper Mich. State Forests
6. Lower Mich. State Forests
7. (Manistee Nat. Forests  
(West central Lower Peninsula

s — More numerous toward south



either rare species or species that are characteristically more common toward the south. Only two species of *Phyllophaga* were collected throughout the entire region. These were *Phyllophaga drakei* (Kirby) and *Phyllophaga anxia* (LeConte). *Phyllophaga gracilis* (Burm.) was collected on all forests in the Lower Peninsula, although it was not listed by Lugenbill and Painter (1953) as a Lake States species. *P. rugosa* (Melsh.), a common species in southern Michigan, was not abundant in the more northern localities although it was collected occasionally in forests of both the Lower and Upper Peninsulas of Michigan. *P. rubingosa* (LeConte) was collected in CCC Camps in all Lower Michigan forests but was not observed by Yeager during his intensive studies in the Huron National Forest. *P. micans* (Knoch), a relatively rare species, was collected on the Huron Forest both at the CCC Camp light collection points and by Yeager. It was observed at no other point in the Lake States. *P. ilicis* (Knoch), a rare species according to Lugenbill and Painter (1953), was collected both in the Lower Peninsula and the eastern end of the Upper Peninsula of Michigan, and a new species, *P. chippewa* (Saylor), described from a single male and possibly an abnormal specimen of *P. knochi*, was collected in Minnesota.

TABLE II — Other *Phyllophaga* Reported by Lugenbill & Painter.

<i>Phyllophaga</i>		
<i>longispina</i> (Smith)		
<i>hirticula</i> (Knoch)	s	Mich.
<i>balia</i> (Say)	s	Mich. & Wis.
<i>villifrons</i> (LeConte)	s	Mich. & Wis.
<i>implicata</i> (Horn)	s	Mich. & Wis.
<i>nitida</i> (LeConte)	s	Mich., Wis. & Minn.
<i>inversa</i> (Horn)		" " "
<i>vehemens</i> (Horn)	s	Mich. & Wis.
<i>fervida</i> (Fab.)		Wis.
<i>spretta</i> (Horn)	s	Mich. & Wis.
<i>bipartita</i> (Horn)	s	Wis.
<i>horni</i> (Smith)	s	Mich.
<i>fraterna</i> (Harris)	s	Mich. & Wis.
<i>forsteri</i> (Burmeister)	s	Michigan & Wis.
<i>prunina</i> (LeConte)	s	Michigan

When full grown the grubs of most *Phyllophaga* species are relatively large. Almost all of the grubs of other genera are small in size. One exception, *Cotalpa lanigera* (L.), is a very common species in north central Michigan but is rare in most other localities. The smaller chafer found in forest plantations are more or less uniformly distributed throughout the Lake States wherever the food plants of the adults occur in abundance. These beetles are listed on Table III.

TABLE III — Non-*phyllophagous* Root-eating Chafer Beetles.

<i>Diplotaxis sordida</i> (Say)	Common
<i>Diplotaxis liberta</i> (Germ.)	Common
<i>Diplotaxis haydeni</i> (LeConte)	Uncommon
<i>Dichelonyx albicollis</i> (Burm.)	On conifers
<i>Dichelonyx elongata</i> (Fab.)	On hardwoods
<i>Serica serica</i> (Ill.)	Abundant
<i>Serica vespertina</i> (Cyll.)	Common
<i>Serica intermixa</i> (Blatch.)	Common
<i>Serica carinata</i> (Blatch.)	Rare
<i>Macroductylus subspinosus</i> (Fab.)	Abundant
<i>Anomala oblivia</i> (Horn)	Common
	jack pine
<i>Cotalpa lanigera</i> (L.)	Common
	to scarce

The large number of potentially injurious species, and their irregular distribution contributes to the complexity of the grub problem. The need for specific information

concerning the habits and injurious proclivities of each species is evident. Much of this work still remains to be done; but the intensive studies in the Huron and Marquette Forests indicate that at least in those parts of the region, only a few species are responsible for the major part of the damage, and that there is a close relationship between the amount of damage and the proximity of suitable food plants for the adult beetles. Similar investigations are needed in other localities.

ROOT DAMAGE CAUSED BY VARIOUS CHAFER LARVAE

In the Huron Forest Yeager conducted a series of experiments to test the food preference of six species of phyllophagous grubs and the grubs of four other chafer genera.

These tests were made in metal containers, approximately 7 inches in diameter and 8 inches deep. Seedlings of pine, oaks, and other species were planted together with grass, in such a manner that all roots were equally available to grubs placed in the containers. The containers were sunk into the soil, partially shaded during hot weather, and regularly watered.

The results are summarized in Table IV. They are expressed as the percentage of each seedling species that was killed by the grubs. As was anticipated, grubs of the

TABLE IV — Seedlings Killed by Grubs Confined near Roots.

	Percentage Killed					
	No. of tests	Larvae per test	Jack Pine	Red Pine	White Pine	Black Oak
<i>P. drakei</i>	18	4	90	88	80	75
	88	3	77	78	72	68
<i>P. gracilis</i>	7	4	75	79	75	50
	48	3	58	52	55	—
<i>P. crenulata</i>	6	4	100	88	75	50
	24	3	58	59	56	—
<i>P. anxia</i>	6	4	100	83	88	50
	25	3	45	48	49	—
<i>P. prunina</i>	1	4	100	100	100	100
<i>P. marginalis</i>	216	3	7	3	3	0
<i>Serica</i> spp.	7	8	18	18	18	0
	100	4	14	13	17	—
<i>Diplotaxis</i> spp.	15	8	20	14	20	20
	50	4	16	15	23	—
<i>Dichelonyx</i> spp.	7	8	0	0	20	0
	15	4	2	2	1	—
<i>Cotalpa lanigera</i>	3	4	0	0	0	0
	25	3	1	0	3	—

Yeager's experiments — Huron National Forest.

genus *Phyllophaga* proved to be more injurious than the smaller grubs of other genera. It was surprising to discover, however, that one species of *Phyllophaga*, *P. marginalis*, and another large species, *Cotalpa lanigera*, caused relatively little injury to the tree roots near which they were confined. Available evidence indicates that these species are not primarily root eaters and that their food may well consist of dead plant materials.

Of the smaller genera, species of both *Serica* and *Diplotaxis* killed some coniferous seedlings, but in nature it is doubtful that they are responsible for much injury. These conclusions are substantiated by a field study in the Marquette Forest where Gross excavated hundreds of recently injured pine seedlings and found only *Phyllophaga* larvae in immediate proximity to the damaged roots. In a few instances, however, *Serica* larvae were within 6 inches of a killed seedling.

From this we may tentatively conclude that, although potentially injurious to pine seedlings, the smaller species seldom cause damage in forest plantations. It must be recognized however, that excessively high numbers of either *Serica* or *Diplotaxis* might occasionally be serious. No such populations were observed during our studies.

REGIONAL PATTERN OF DAMAGE BY GRUBS: During the general regional survey of CCC Camps in 1934 it was observed that tremendous variation characterized amount of grub injury in plantations. These local variations tended to obscure the general regional pattern.

Not until the more intensive survey was made in 1935, was a significant regional pattern revealed. The most severe damage was in plantations in the Marquette Forest where almost every plantation suffered serious damage. Farther west in the Upper Peninsula the losses were much less severe. In the Ottawa National Forest, for example, and in the adjacent forests in Wisconsin, grub injury, although serious in some plantations, was generally light. Similarly in Minnesota, although severe locally, many plantations were very little affected by grubs. In the Lower Peninsula of Michigan, plantations in the Huron Forest on the eastern side of the State, although less severely damaged than those in the Marquette, suffered far more heavily than did the State Forests to the west. The Manistee Forest on the west side of the Lower Peninsula suffered least of all, although a few individual plantations in that forest were severely damaged, and the forest nursery was heavily infested by grubs.

What influences could cause these regional differences? It is dangerous to generalize when considering such extensive and diverse areas, but sometimes a broad view discloses situations that are obscured when only local conditions are considered.

Let us first compare two extremes of damage; the Marquette Forest and the Ottawa and northern Wisconsin group. There is a striking difference in one respect. The Marquette was predominantly made up of deforested land. For the most part the soils were light and sandy. From some locations the denuded areas extended as far as the eye could see. But these lands, though open were spotted with small birches and an occasional aspen clone. In contrast, the lands included within the Ottawa and northern Wisconsin forests were diversified, both as to soils and forest cover. The light sandy soils comparable to the predominantly open conditions on the Marquette were far less extensive, and more completely forested. It seems likely from our studies that these conditions might limit chafer populations.

The Huron Forest which ranked second to the Marquette in degree of grub damage, was in part a comparatively open forest. The openings, however, were smaller and spotted with scattered individual trees, mostly oaks and jack pine instead of the birches and aspens of the Marquette plantations.

The State Forests, both in the Upper Peninsula and in the Lower Peninsula, tended to be more diversified than the Huron and Marquette. Similarly the Minnesota forests had a much smaller complement of denuded lands than did the Marquette. Thus there seems to be a definite correlation between grub damage and the extent of denuded forest lands in a locality.

INFLUENCE OF VEGETATION ON GRUB CAUSED DAMAGE: The region-wide survey of young pine plantations made in 1935 disclosed a clear relationship between the losses caused by grubs and the vegetative cover. It was obvious that the arboreal food plants of the adult beetles wielded a great influence, but considerable injury frequently occurred in places where few if any trees were present. In these instances shrubs provided the beetles with food.

The data have not been completely analyzed but the following four tabulations give some idea of the influence which vegetation and particularly the combination of some plant species can have upon the amount of damage by white grubs.

In Tables V, VI, VII, and VIII the species with which the others are combined is listed on the top line. The quantities in each column represent the percentage of the plots containing that species which were injured by the grubs to the degree indicated at the head of each column. In each subsequent line is shown the percentage of plots damaged to the indicated degree when the plant listed in that line occurred in combination with the tree listed in line one. A markedly higher percentage of injury than that shown in line one (figures shown in *italics*) would indicate a combination especially conducive to grub damage. This might be a direct or indirect effect. For example, the large percentage of damaged plots observed when black oaks and goldenrods are combined, might either be due to the presence of goldenrods in combination with

black oaks, or to the presence of some other plant or condition usually associated with goldenrod.

There is some indication that the combination of favored woody food plants with herbaceous species characteristic of openings, is correlated with high damage. However, the number of *Phyllophaga* grubs both in the Marquette and Huron forests were on the average higher in closed stands than in the open, in spite of the fact that injury to the trees was inversely proportional to the density of tree stocking. This apparent inconsistency was evidently due to the failure to distinguish between the woodland species *P. marginalis*, which eats few roots, and the *Phyllophaga* which are voracious root eaters. This points out that estimates of grub populations which fail to distinguish between harmful and innocuous species may have little value.

TABLE V — Combinations with White Oaks.

	Percentage of plots damaged			
	Huron 10% +	Marquette 30% +	Minnesota 10% +	Michigan State Forests 10% +
White Oaks (all plots)	33	80	43	10
Black oaks	29	—	26	9
Sedges	28	—	50	9
Ferns (Bracken)	34	80	34	8
Lichens	33	80	57	4
New Jersey tea	—	—	63	17
Sod grasses	—	—	55	12
Bearberry	35	—	56	9
Rose	33	—	47	10
Hazel	—	—	43	50
Shrub cherry	29	—	45	4
Asters	—	—	49	25
Goldenrods	—	—	47	9
Wintergreen	—	—	57	12
Willows	43	—	46	—
Pearly everlasting	—	—	54	1
Aspen	24	—	39	13
Juneberry	48	—	42	9
Blueberry	—	80	42	9
Birch (white)	—	—	32	—
Honeysuckle	—	—	34	2
Sweetfern	—	—	—	9
Alder	—	—	11	—
Red Maple	—	—	11	8
Bunch grass	34	—	28	9
Mixed herbaceous	—	—	33	15
Raspberry	—	—	25	—
Fireweed	—	—	15	10

— Indicates data lacking or considered inadequate

FOOD PLANTS OF THE MORE COMMON ADULT CHAFERS: Observations made during our study in the Lake States indicate clearly that few species of chafers are narrowly restricted in their feeding. The majority eat the leaves of broadleaved trees and shrubs, but some eat coniferous needles and others eat herbaceous foliage. Table IX lists the food plants growing in the Lake States on which 8 common *Phyllophaga* beetles are known to feed. In this table the letter "L" indicates that the report is listed by Lugenbill & Painter (1953) and "S" that feeding was observed during our study.

The wide range of food plants is discouraging until one realizes that all the plants listed are not necessarily highly favored. They merely represent field observations sometimes of a casual nature. Unfortunately there is little quantitative evidence available to indicate food preferences of the various species; and without such information we are at a loss to evaluate the relative influence of the reported food plants.

In the Huron National Forest Yeager, over two seasons, 1935 and 1936, collected some quantitative information concerning three *Phyllophaga*. He recorded the number of feeding beetles observed each night on nine plant species. The results are presented in Table X. The data are expressed in the number of beetles per night on 10 lineal feet of foliated branch examined.

A part of the preference exhibited by the species included in Table IX is seasonal. For example *Phyllophaga drakei*, in the Huron forest feeds on aspens early in the season. Later it transfers its activity to juneberry, and still later to black oaks. In the Marquette Forest it transfers from aspen to white birch and the combination of these two species is especially favorable for high *P. drakei* populations.

*P. gracilis*, on the other hand, emerges later in the season and flies for only about twenty days. Black oaks provide suitable succulent foliage throughout the flight period,

TABLE VI — Combinations with Black Oaks.

	Percentage of such plantations damaged			
	Huron 10% +	Marquette 30% +	Minnesota 10% +	Michigan State Forests 10% +
Black Oaks (all plots)	37	55	32	7
Sedges	36	34	40	7
Ferns	33	33	31	6
Grustose lichens	35	36	26	6
New Jersey tea	38	—	49	—
Sod grasses	54	—	43	10
Bearberry	41	—	49	8
Rose	33	—	33	10
Hazel	53	—	34	2
Shrub cherry	38	—	31	4
Asters	25	—	39	17
Goldenrod	46	57	40	5
Wintergreen	49	—	35	5
Willows	33	39	33	9
Pearly everlasting	—	—	45	6
Juneberry	45	—	30	6
Aspen	43	61	82	7
Blueberry	37	33	34	6
Birch (white)	—	60	28	—
Honeysuckle	—	—	31	2
Sweetfern	36	28	15	6
Alder	—	—	10	—
Red maple	47	27	10	5
Bunch grass	36	44	13	7
Mixed herbaceous	70	21	16	8
Raspberry	—	—	14	7
Fireweed	—	—	12	

— Indicates data lacking or considered inadequate

although the beetles supplement their black oak food with the foliage of New Jersey tea. *P. crenulata* emerges early, feeds first on juneberry, then on black oaks, and finally on New Jersey tea. It is not surprising that New Jersey tea is likely to be associated with a high percentage of grub injury to the planted trees, since it produces succulent foliage late in the season.

*P. drakei*, is favored by presence of scattered aspens and birches in mixture and is the most injurious species in the Marquette Forest. The abundance of black oaks and the relative scarcity of birch in the Huron apparently explains why *P. drakei* is relatively scarce there, where *P. crenulata* and *P. gracilis* find conditions more favorable. A similar succession of foods was observed for various other species.

A more precise test of food preferences of adult beetles was conducted with caged beetles presented with foliage of various kinds so that each was equally accessible.



Table XI summarizes the result of these experiments. The amount of each plant eaten is tabulated as the percentage of the total foliage presented.

It is interesting to observe that some trees and shrubs on which beetles were frequently collected in the field, proved to have a lower preference rating under experimental conditions, where a free choice could be exercised. This apparent inconsistency may be explained by the fact that second or third choice foods may be more available to the beetles in the field than those with a higher rating. As a result they fed upon these common plants more frequently than would be expected from experiments in which all foods were equally available. It seems likely, however, that plants with the high experimental rating might influence population increase more than would those that are less preferred.

TABLE VII — Combinations with Aspens.

	Percentage of such plantations damaged			
	Huron 10%+	Marquette 30%+	Minnesota 10%+	Michigan State Forests 10%+
Aspens (all plots)	37	58	27	7
Black Oaks	43	61	82	7
Sedges	37	80	42	5
Ferns (Bracken)	40	59	24	7
Lichens	39	65	24	6
New Jersey tea	43	—	63	—
Sod grasses	42	—	39	9
Bearberry	46	—	32	11
Rose	37	—	30	8
Hazel	50	—	28	17
Shrub cherry	37	67	29	5
Asters	60	—	28	22
Goldenrod	65	66	28	6
Wintergreen	35	—	28	4
Willows	36	68	27	8
Pearly everlasting	—	—	—	7
Juneberry	47	79	27	8
Blueberry	39	62		4
Birch (white)	—	68	24	9
Honeysuckle	—	51	20	5
Sweetfern	37	73	23	7
Alder	—	—	20	0
Red maple	42	72	19	8
Bunch grass	40	79	16	6
Mixed herbaceous	—	44	17	10
Raspberry	—		17	4
Fireweed	—	90	15	8

— Indicates data lacking or considered inadequate

This idea is supported by our observations that *Phyllophaga drakei* is especially numerous in localities where birch and aspen are growing together, and scarce in localities where aspen is growing alone, in spite of the fact that aspen is recognized as a common food plant for the species.

Another point seems clear from the preference tests summarized in Table XI. Red oaks are highly favored by all six of the species tested, and field observations throughout the Lake States show a high correlation between oaks and grub damage.

GRUB NUMBERS UNDER DIFFERENT CONDITIONS: From the region-wide survey it was clear that vegetation on and adjacent to a certain plot influenced the amount of injury by grubs; but variations in both the species of chafer present, and the plant and soil combinations, caused difficulty in drawing fully acceptable conclusions. Therefore, in the Huron Forest, Yeager conducted some intensive examination of soil

samples for grubs, carefully supervising the work and personally examining all grubs collected. His results are presented in Table XII.

It will be a surprise to some entomologists that grubs were found in areas of blow sand where they must have been feeding on roots invading the bare places from the side or on the small amounts of organic material in this almost sterile soil. Numerous observations, made in the course of our studies, contradict the statement frequently found in literature to the effect that phyllophagous beetles prefer to oviposit in grass lands.

From our work we are led to conclude that the proximity of suitable food for the adults exercises a far more significant influence than does the kind of herbaceous vegetation.

TABLE VIII — Combinations with White Birch.

	Percentage of such plantations damaged			
	Huron 10% +	Marquette 30% +	Minnesota 10% +	Michigan State Forests 10% +
White birch (all plots)	—	76	24	7
Black oaks	—	60	28	18
Sedges	—	64	39	11
Ferns	—	77	23	12
Lichens	—	81	17	28
New Jersey tea	—		58	—
Sod grasses	—	—	34	—
Bearberry	—		25	—
Rose	—		26	—
Hazel	—		24	—
Shrub cherry	—	90	25	7
Asters	—		24	
Goldenrod	—	83	24	11
Wintergreen	—		27	10
Willows	—	82	24	19
Pearly everlasting	—		22	—
Aspen	—	68	25	10
Juneberry	—	85	25	—
Blueberry	—	84	24	16
Honeysuckle	—	81	19	7
Sweetfern	—	81	9	12
Alder	—		19	
Red maple	—	78	20	7
Bunch grass	—	84	20	12
Mixed herbaceous	—	70	9	—
Raspberry	—	—	18	—
Fireweed	—	89	14	—
White oaks	—	—	32	20

— Indicates data lacking or considered inadequate

OVIPOSITION WITH REFERENCE TO FOOD PLANT DISTANCE: Obviously the beetles are capable of flying long distances, but, if we are to accept the evidence of Yeager's intensive observations, they seem to move about very little during oviposition. For example, some marked beetles were observed feeding night after night on the same small tree or shrub and presumably must have passed the days in the soil immediately below.

In order to determine the influence of nearby food upon the local distribution of grubs, soil samples at different distances from food plants were carefully examined. The results were striking. The grub population of all genera taken together declined from 16 per ten square feet immediately under broadleaved food plants to 2 per ten square feet at a distance of 50 feet. At 200 feet practically no grubs of any kind could be found. Phyllophagous larvae were seldom found at distances greater than

TABLE IX — Food Plants of more Common Adult *Phyllophaga*.

	<i>P. drakei</i>	<i>P. gracilis</i>	<i>P. marginalis</i>	<i>P. anxia</i>	<i>P. rugosa</i>	<i>P. crenulata</i>	<i>P. rubingosa</i>	<i>P. prunina</i>
Black Oaks	S	S	S					
Aspens	S					S		
White Birch	S					S		
Birches	L		L		L			
Juneberry	S	S				S		
Rose	L	S	L	L	L	L	L	L
Willows	LS			L	L	L		L
Elms	L		L	L	L	L	L	L
Witch hazel	L		L	L	L	L		L
Dogwoods	L			L	L	L		
Honeysuckle	L					L		L
Basswood	L			L	L	L		L
Beech	L	L	L	L	L	L		L
Maples	L		S	L	L			
Legumes		L			L	L		L
New Jersey tea			L			S		
Compositae				L	L			
Lily						L		
Sumac						L		
Cherry	S			S		S		

L = Lugenbill & Painter (1953)  
S = Current Study

TABLE X — Food Preferences of Three Adult *Phyllophaga*.

	Beetles per 10 lineal feet of foliated branch		
	<i>P. drakei</i>	<i>P. gracilis</i>	<i>P. crenulata</i>
Black oaks	2.33	22.88	1.03
White birch	3.00	2.63	5.64
Aspens	1.42	0.00	0.00
Juneberry	1.01	8.50	14.71
New Jersey tea	0.14	2.23	4.78
Rose	0.42	1.37	0.42
Cherry	0.10	0.00	0.00
Willow	1.41	0.00	0.00

100 feet, whereas grubs of the genus *Serica* occurred much farther from the beetle's food plants.

Similarly, the grubs of beetles which eat coniferous foliage were most numerous adjacent to the food trees, ranging from an average of a little more than 5 per ten square feet immediately under jack pine to less than one at a distance 50 feet. These results are striking and point to the possibility of white grub control through the regulation of adult-food plants.

ANALYSIS OF THE GRUB PROBLEM: It is evident from our study of white grubs in forest plantations, that the problems involved are by no means simple. Complexity arises because of the number of potentially injurious species that are involved and the differences in their food habits. Records of food plants for the various species are helpful but are not critical enough to guide cultural practices. It is not enough to observe that a species feeds upon certain plants. The relative preference for the various

TABLE XI — Food Preferences of some Caged *Phyllophaga*.

Percentage of total food presented that was eaten						
	<i>P. drakei</i>	<i>P. gracilis</i>	<i>P. crenulata</i>	<i>P. marginalis</i>	<i>P. anxia</i>	<i>P. prunina</i>
Black oaks	58	43	26	36	39	64
	19	25	17			
White birch	22	27	22	23	0	
Aspens	2	1	2	4	10	1
	5	6	3			
Juneberry	45	26	45	16	16	22
	27	18	27			
New Jersey tea	18	19	17	17	13	6
	13	13	12			
Rose	9	11	9	1	8	5
	11	10	11			
Cherry	1	0	1	0	1	1
	1	0	1			
Willow	1	0	1	0	9	tr*
	1	1	1			
Blueberry	5	0	0	1	0	0
		2	5			

\* Trace

potential foods must be known before the relative influence upon grub populations of each food can be evaluated. This information is available for only a few species.

The destructive potentialities of only a few species have been tested, but even these few tests have shown that two species, *P. marginalis* and *Cotalpa lanigera*, previously assumed to be noxious, appear to be relatively innocuous. Careful study may reveal that other previous assumptions have been incorrect so that other species may fall into the innocuous category. Generally speaking, our observations strongly

TABLE XII — Abundance of Chafer Larvae under Different Conditions.

Grubs per ten square feet							
Vegetational types	Sq. ft. sampled	<i>Phyllophaga</i>	<i>Serica</i>	<i>Diplotaxis</i>	<i>Dichelonyx</i>	<i>Macroductylus</i>	<i>Cotalpa</i>
Bog shrubs	24	0.00	0.00	0.00	0.00	0.00	0.00
Cedar-spruce seepage	48	0.00	0.00	0.00	0.00	0.00	0.00
Alder-willow	80	0.37	0.38	0.00	0.00	0.00	0.00
Bare sand	80	0.88	0.50	2.12	0.00	0.00	0.00
Opening in oak-aspen	224	1.07	2.10	0.00	0.67	0.00	0.13
Jack pine-blueberry	344	0.78	2.03	0.41	0.41	0.58	0.00
Jack pine-New Jersey tea	144	1.11	2.30	0.49	0.07	0.62	0.70
Jack pine-bunch grasses	326	1.50	2.14	1.05	0.05	0.70	0.23
Oak-maple-aspen	460	*5.20	8.59	0.00	0.41	0.26	0.00
Oak-sweetfern	152	1.52	12.57	0.07	3.86	0.00	0.00
Black-white oak	454	4.23	10.95	0.00	2.58	0.71	0.00
Aspen	80	0.75	26.50	0.00	6.00	0.00	0.00
Aspen-white birch	180	1.06	16.94	0.00	21.74	0.00	0.00

\* Mostly *P. marginalis*

Adapted from Yeager

indicate that species of *Phyllophaga*, and to a lesser degree *Serica* and *Diplotaxis*, are likely to be injurious to planted pines.

The long life cycle and the resultant periodic peaks of injury during years when the phyllophagous larvae are in the most voracious stages deserve far more careful study than has thus far been possible. Evidence from the Marquette Forest indicate definitely that *P. drakei* passes through a five-year life cycle in that northern region, and that flights of adults are less regularly spaced than might be expected, because of overlapping broods. Furthermore, in spite of the long, cold winters which characterize northern Michigan, a large proportion of the larvae of *P. drakei* pass the winter within 12 inches of the soil surface.

Our studies show rather clearly that oaks and white birch are commonly associated with damage to planted trees, and that the presence of some shrubs such as juneberry and New Jersey tea are also conducive to high grub populations. Further analysis of data and the completion of the long-term study of vegetational changes on the Huron Forest should amplify our understanding of how vegetation influences grub numbers and how the environment may be modified to bring about grub control. The belief that control of white grubs by cultural practices is possible, is strengthened by what we have learned about the oviposition habits of the beetles which seem to deposit most of their eggs within a hundred yards of their food plants. This knowledge can be turned to good advantage in nursery practice where a barrier belt free of favored food plants could almost eliminate grub injury.

The practicability of this was demonstrated clearly in a nursery on the Huron Forest where the removal of a few large oak trees brought about perfect control of grubs.

Grub damage is correlated with weather variations, dry weather being associated with relatively severe damage. We assume that this is due to the lower resistance of planted trees to root injury during such seasons, but the possibility that direct effects of moisture are also operating upon the grubs should not be disregarded.

### CONCLUSION

In concluding this discussion of white grubs and other forest insects several points are worthy of comment. Some insects such as the grubs have always been recognized as important pests of young trees. Many others have not hitherto been injurious and have only become common since forest plantations have been set out over vast areas. The problems caused by these latter species in forest plantations in the Lake States are of our own making. We have set the table for these pests by excessive planting of the same tree species on large contiguous areas. We may expect that new species will continue to appear as the plantations pass from saplings to pole size.

Emergencies arising from these insects must be met promptly and may require direct treatment with insecticides if the plantations are to be protected. However, it seems clear, at least to some foresters and forest entomologists that many of our problems can in the future be solved by silvicultural practices that will create conditions less conducive to insect outbreaks than those of today. These practices will require planning and must be based upon a thorough understanding of the insects themselves and the tree species on which they feed.

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### DISCUSSION

H. A. RICHMOND. In relation to the upsurge of plantation insects could there be any direct relationship to the extension of nursery plantations over areas of poor site for the tree species concerned?



S. A. GRAHAM. Most sites on which pine plantations have been established previously grew pines. Therefore, one would not expect that the upsurge of new species is related to poor site. We must recognize, however, that fires following logging might have affected the site adversely, and reduced quality appreciably.

J. J. FETTES. In view of the seriousness of insect damage to tree roots in plantations, has it been considered that treatment with soil insecticides might be recommended as standard practice?

S. A. GRAHAM. This has been recommended and tested on an experimental scale. They appear to afford protection for a year or possibly more. How effective soil insecticides would be under excessively dry conditions such as those that prevailed in the mid-thirties, is problematical.

# Chemical Control of Forest Insects by Aircraft in Sweden

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## ABSTRACT

Application of insecticide dust from aircraft was first launched against forest pests in Sweden in 1944. The step was taken against the pine looper (*Bupalus piniarius*) which attacked a pine forest in the south of Sweden. On this occasion about 1,000 hectares (2,500 acres) were dusted from airplanes with 5% DDT at about 7 kg/hectar (6 lbs/acre). In spite of this small quantity of poison being used a good result was achieved (96% mortality).

Since this first attempt, dusting from airplanes has been tried several times under different circumstances, usually with satisfactory results. The method was less effective when it was applied to nest-building insects, for example, *Cephaelea abietis* and *Tortrix viridana*. Latterly the dusting method has undergone certain changes intended to make results more effective. Thus at an early stage ordinary airplanes were replaced by helicopters, these machines having important advantages: they are easier to manoeuvre and are less sensitive to thermic disturbances, thanks to the ability of the rotor to press the dust down into the crowns of the trees.

The insecticide most usually employed in Sweden is DDT (dosage 9-18 lbs/acre), sometimes mixed with BHC.

Spraying with poisons from the air against forest insects has not been made use of to any great extent in Sweden, although this method of application is more effective than dusting. The reason is that the authorities wish to diminish the killing effect of DDT on other insects in forests, and therefore use dust which is less adherent.

The signalling system applied in Sweden is characterized by its mobility: big balloons are moved along so-called balloon lines as the work advances. These lines run at right angles to the line of flight.

In order to determine whether a given method for fighting insects, such as dusting, may or may not be suitably employed, it is necessary to know whether the initial outbreak is likely to continue, and if so, its probable extent and intensity.

Investigations undertaken with a view to evolving simple and reliable methods of prediction, were first put in hand in Sweden in 1944 in connection with the large-scale outbreaks of the pine looper (*Bupalus piniarius*). The method evolved during these outbreaks has been improved in recent years. This method applies exclusively to insect pests which hibernate under litter as pupae or larvae. It consists of the examination of sample plots within the infected area along parallel survey lines. The spacing between the sample plots and between the survey lines varies according to the degree of accuracy desired. Usually the spacing between the lines is 100 metres, and between the sample plots 50 metres. The size of the sample is as a rule 50 x 50 cm. They are investigated as follows. The litter is first removed, whereupon the humus is carefully sifted down to the mineral soil for pupae and larvae and also for empty pupal capsules. The number of pupae is recorded for each sample plot in a special register. At the conclusion of the survey a general view of the distribution and abundance of the pest is obtained. The figures for abundance cannot be used, however, as a basis for estimating the population density in the following year. The decisive point in this connection is not the total number of pupae, but the number of healthy pupae. Thus, it is necessary after every survey to examine the collected pupae in regard to their condition. In the course of this examination a distinction is drawn between pupae infected by fungi, bacteria or virus and healthy pupae. Only after determining the percentage of healthy pupae is it possible to assess the extent of the pest during the coming year with a fair degree of reliability. Experience has shown that when the population density of a species reaches a given value, defoliation of a stand may be anticipated. This value is known as the critical number for the pest and is decisive in assessing every outbreak. When the method of prediction was first employed in Sweden

no local critical numbers were available for reference and it was therefore necessary to rely upon figures obtained from experience abroad, primarily in Germany. Swedish entomologists have been working steadily with the object of establishing critical numbers for pests under domestic conditions and their work has been successful insofar as some of the important forest insects are concerned. In distinction to the critical numbers employed in Germany which relate to a population density sufficient to destroy half of the needles or other foliage, we have adopted values which relate to total defoliation.

The results of the entomological surveys are entered on a map, thus enabling a distinction to be drawn between the different abundance zones above and below the critical number. A map of this kind serves as a basis for every pest fighting campaign.

Methods of controlling outbreaks of primary forest pests have represented a source of considerable trouble both for the forest entomologists and for practical workers in the field. During outbreaks of defoliators, control methods formerly employed cannot be regarded as satisfactory from the point of view of efficiency. In the course of the catastrophic outbreaks of the nun moth and gipsy moth in 1898-1902 for example, both glue belts against larvae and tar preparations against eggs were employed. Both methods are very time-consuming and call for an extensive labour force. Moreover, the costs which these methods entail are so high that they can scarcely be regarded as economically justifiable under present-day conditions.

When outbreaks of such insects as pine loopers, pine sawflies and others occurred, no measures of any kind were available for controlling them and we had to allow the devastation of these pests to go unchecked.

By the middle of the 1920's a number of new methods for controlling acute outbreaks of forest pests had been tested in several European countries and in North America. These methods consisted of spreading insecticides either from aircraft or from the ground by means of motor dusters. For this purpose insecticides designed to operate as internal poisons were employed, amongst which certain arsenic salts were the principal constituent. After a few years of experimentation the method had been improved to such an extent that it could be employed on a wide scale under field conditions. It is true that dusting was hampered by certain drawbacks such as the risk of poisoning useful animals, the danger of the powder being washed away by rain, etc.; nevertheless forest owners have now been provided with an effective weapon in their fight against even the most dangerous forest pests.

In Sweden experiments for testing the new method of control were carried out at a much later date. During the 1930's, repeated applications were made by the Zoological Department of the Forest Research Institute for a grant to enable experiments to be carried out with the dusting method under Swedish conditions, and thus to establish a means for dealing with imminent catastrophes. These applications for funds led to no result, however, as the government authorities did not consider the problem to be of immediate interest. It was only in the year 1944 after very extensive areas of pine forest had been severely attacked by the pine looper that the government provided the means for a campaign against this pest in view of the threatening situation in the forest concerned. At the same time the Zoological Department was entrusted with the task of organizing, directing and supervising the campaign. However, the work of organization was hindered appreciably by the military situation at that time. It was not possible to obtain any specially constructed aircraft or dusting equipment. Consequently, the Department was obliged to rely upon the assistance of Swedish firms for the construction of suitable dusting equipment based on special articles published abroad. This equipment subsequently underwent a number of improvements and could be employed under practical conditions although it could not be regarded as entirely satisfactory from a technical point of view. The type of aircraft first used was a hydroplane (Junker W 34). The question of the insecticide and the dosage also caused considerable difficulty. The insecticides previously used abroad against forest pests consisted of arsenic salts, namely arsenates in Western Europe and arsenites in the USSR. The former called for a dosage of 50-100 kg per hectare and the latter 5-15 kg per hectare.

According to the existing regulations relating to poisons, forest dusting with arsenic must not be carried out unless edible berries, mushrooms, etc. are covered over while

dusting is in progress. These regulations precluded the use of arsenic for the campaigns in question. In place of arsenic powder, therefore, it was decided to experiment with the contact insecticide DDT which had only been recently discovered, although it had not been previously used for forest dusting. This implied that the campaign leaders possessed no experience to guide them with respect to the dosage, adherence, etc. This insecticide nevertheless appeared to be very promising on account of the high toxic effect it was found to have on pine looper larvae during preliminary tests.

The first dusting campaign was carried out during the period August 24 to September 8, 1944, in the course of which a total area of 1300 hectares was treated. The average dosage was about 7 kg per hectare. The mortality amounted to about 96 per cent which in view of the small dosage could be regarded as an extremely satisfactory result.

A further dusting campaign for the suppression of the pine looper was undertaken in the course of the year 1945 with an aircraft of the Focke S6 type.

A new method of signalling was also evolved in connection with dusting. The essential feature of this method was that the signals were mobile. Marking balloons hoisted up on balloon cables were gradually moved forward while dusting was in progress. This method of signalling represented a considerable advance over stationary marking at the corners of the dusted area as employed on the continent.

Notwithstanding the successful results achieved in the first dusting campaigns, the method tested was found to possess numerous disadvantages.

Since standard aircraft are dependent upon relatively long take-off and landing runways, the landing ground must often be located at some considerable distance from the area of operations, which renders communication between the pilot and headquarters more difficult and also increases the cost of operation. Thermal disturbances and wind conditions likewise add appreciably to the difficulties of dusting, since they reduce the effective working time to a minimum; usually a few hours in the early part of the morning. When further dusting campaigns were planned to combat different species of pest in 1947 the Zoological Department decided to abandon the use of conventional aircraft and experiment with a helicopter of the Bell 47B type which had recently undergone a number of tests for dusting in the United States with successful results.

The first attempt at forest dusting from a helicopter, which incidentally was also the first occasion on which the method was used in Europe, was made in 1947 at Visingsö in South Sweden, against the winter moth (*Operophtera brumata*), birch cankerworm (*Operophtera fagata*), oak leafroller (*Tortrix viridana*) and other pests. The results were very satisfactory from a technical point of view. The helicopter's manoeuvrability was excellent and the speed could be regulated in accordance with requirements, thus permitting a smooth and uniform treatment of the canopy. Taking off and landing were possible even on small open spaces which greatly facilitated the work and enhanced the performance. A further very substantial advantage was found in the capacity of the rotor to press down the dust cloud into the canopy. Thanks to this property the disturbing effects of heat and wind could be counteracted. This was accompanied in turn by an appreciable increase in the working time and an improvement in the performance. It was only necessary to discontinue the work of dusting during the warmest period of the day or in strong winds and, of course, in rainy weather.

Experimental dusting from a helicopter was nevertheless found to be accompanied by certain disadvantages. For instance, the loading capacity of these machines is small in comparison with that of larger aircraft. Moreover, the costs for dusting are higher than is the case with an ordinary aircraft and in addition, the helicopter is more easily damaged and requires frequent overhauling and inspection. The advantages of this type of aircraft are so outstanding, however, that they more than outweigh its drawbacks. For these reasons helicopters have been used exclusively in Sweden for forest dusting since 1947.

The method of dusting from aircraft adopted in Sweden — now that extensive areas of forest have been treated in this way — may therefore be regarded as suitable for use under practical forestry conditions. It has not been possible, however, to control all forest pests with complete success by means of air dusting. For instance, repeated

TABLE I — Air Dusting in Swedish Forests During the Period 1944-1950.

Year	Date	Place	Area hectare	Total weight of dust in kg	Type of Aeroplane	Dusting carried out by (company)	Total costs Sw. Crs.	Pests
1944	24/8-30/8	Hökensås	965	6.875	Junker W 34	AB Flygtjänst	32.500	Bupalus piniarius
1944	4/9	Skyllbergsbruk	205	1.700		"		"
1944	7/9	Påla Malm	100	750	Junker W 34	"		"
1944	8/9	Hamra Malm	20	74	"	"		"
1945	12/8, 15/8 17/8	Hökensås	228	1.596	Focker S6	"		"
1947	11/6-12/6	Visingsö	715	10.900	Bell-47B-3 (Helicopter)	Basbolaget	25.530	Operophtera brumata
1947	11/7	S:t Olof	190	4.150	"	"	8.000	Cephaleia abietis
1947	"	Kronovall	100		"	"	4.200	"
1947	"	Kristinehov	100		"	"	4.200	Panolis flammea
1947	9/7-10/7	Vittskövle	100	1.650	"	"	33.000	Lymantria monacha
1948	/5	Visingsö	750	12.000	"	"	45.100	Operophtera brumata
1948	13/6-14/6	Vittskövle	1.025	13.000	"	"	16.280	Panolis flammea
1948	15/6	Vanneberga	370	5.525	"	"	9.240	Lymantria monacha
1948	17/6	Vassmolösa	210	3.200	"	"	313.500	"
1948	/6-7	Hökensås	7.125	103.150	"	"	12.696	Panolis flammea
1949	26/5	Perstorp	276	4.140	"	"	7.728	"
1949	28/5	Konga prästg.	35	525	"	"		Hybernia defoliaria
1949	"	Knutstorp	168	2.520	"	"		Hybernia defoliaria
1950	11/7-12/7	S:t Olof	175	3.125	"	"	12.075	Cephaleia abietis
1950	12/7-14/7	Kronovall	195	4.750	"	"	13.455	
1950	"	Kristinehov	155	3.125	"	"	10.695	



attempts to control the spruce sawfly (*Cephaleia abietis*), and to some extent *Tortrix viridana*, have not yielded satisfactory results, notwithstanding an increased dosage and a higher DDT-content. This is due to the fact that the larvae of these species live under more or less protected conditions in spun nests.

The dusting campaigns carried out during the period 1944-1950 under the direction of the Zoological Department are listed in Table I.

From 1944 to 1948 forest dusting was undertaken voluntarily, that is to say, at the request of the respective forest owners. These dusting campaigns were paid for by the State in most cases. Since the 1st January 1949, however, when a new law relating to silviculture came into force the situation has undergone a considerable change. According to Par. 34 of this law, in the event of extensive outbreaks of forest insects or where a risk of such outbreaks exists, the forest owner is under obligation to carry out the measures prescribed by the Forestry Commission after consultation with the Forest Research Institute. The State makes a reasonable contribution towards the defrayment of the costs. In practice this contribution amounts to at least 50 per cent of the costs.

Financing of the control measures is further facilitated, thanks to certain forest-fire insurance companies who have introduced a new form of insurance since 1949 by which every forest owner who has taken out fire insurance on his forest receives a contribution towards the cost of control measures carried out according to Par. 34 of the silvicultural law. Where a forest is fully insured this contribution corresponds to the difference between the total costs for the campaigns and the amount contributed by the State.

## DISCUSSION

J. S. YUILL. Why do you use dust instead of spray?

V. BUTOVITSCH. In order to diminish the mortality of other insects and animals in the forest.

J. S. YUILL. Have you used helicopters in dusting areas of rough terrain and high altitude? We have found that performance of helicopters is greatly reduced at higher elevations.

V. BUTOVITSCH. No.

F. P. KEEN. What is the approximate cost per acre of dusting in Sweden?

V. BUTOVITSCH. About 40 to 50 Swedish krona per hectare or 3 to 3½ dollars per acre.

R. E. BALCH. Do you get a resurgence or quick rise in the population after spraying?

V. BUTOVITSCH. No, the outbreaks of the winter moth have not reappeared until four or five years after the treatment.



# Problems of Forest Aerial Spray Dispersal and Assessment<sup>1</sup>

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## ABSTRACT

*This paper deals primarily with the problems of forest aerial spraying and some inadequacies of present methods of dispersal and assessment. Many of the factors have been investigated to a point or have been adequately treated for crop-spraying techniques only. More comprehensive experimentation is indicated if forest spraying is to gain the sound bases required. Toxicological studies of forest insects, particularly the species important in the northern part of North America, are few. Such studies are needed to provide guides to insecticides and formulations for field control studies. Evaporation of air-borne spray droplets causes important changes in insecticide concentrations and the behaviour of spray clouds. Concentration changes have a bearing on toxicity. The meteorological aspects of aircraft spraying have been investigated for crop application. The principles of air currents and temperature gradients applicable to crop spraying have been applied to forest spraying, sometimes unwisely. Insecticide deposit has been measured by several methods all of which have some failings. These inadequacies and part of their correction are reported. A precise definition of adequate and efficient dosage of insecticides for the control of forest pests cannot yet be made. These phases of forest insect spraying are discussed and the direction of future investigations is suggested.*

## INTRODUCTION

The application of chemicals to forested areas for the control of destructive forest insects has become relatively commonplace in recent times. Biological and cultural methods for the correction of insect population imbalance are being studied and it is hoped that many of the conditions responsible for the development of destructive outbreaks will eventually be determined so that remedial steps can be taken. However, until such methods are available it will be necessary to use the drastic and expensive means of direct chemical control as an emergency measure for the protection of valuable forests from destructive insect epidemics.

Spray methods now in use have evolved from numerous field tests reported from many parts of the world. A large proportion of our knowledge has been borrowed from experiences in crop spraying and adapted to the widely different conditions obtaining in forest insect control problems. Such adaptations are sometimes based on gross assumptions which are not necessarily valid and therefore may lead to unsound methods and conclusions.

Several aspects of application and assessment problems, although recognized by many writers, have not been intensively investigated, possibly due to a lack of appreciation of their importance. Foremost, are the problems of evaporation and deposit measurement. Other aspects such as toxicological considerations and meteorological problems are interrelated with the above, but are no less important.

This paper deals with the problems of spray dispersal and assessment which are peculiar to forest spraying. Most of the aspects refer to problems of experimental spraying and not necessarily those of large-scale commercial spray operations, except, indirectly, as they affect spraying and assessment techniques. It is not proposed to discuss those aspects of forest aerial spraying already adequately covered in the literature.

## EVAPORATION

Sprays containing volatile liquids are, of course, subject to evaporation upon exposure to the atmosphere. In crop spraying, volatility is not a serious drawback because the droplets are exposed for but a short period before coming into contact with the target. In forest spraying, however, where the droplets are emitted 100 feet, or more, above the target, evaporation plays an important role indeed.

<sup>1</sup>Contribution No. 366, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

Early in forest spray work, emulsions and water suspensions were abandoned because of the rapid loss of the fast-evaporating water fraction. This caused the majority of the drops to shrink below the size that would settle, or even result in dry dust particles which would not remain on the tree foliage. Recently, however, in aircraft spray trials on Vancouver Island, B.C., where the relative humidity was consistently high (90% RH), oil formulations, in which an emulsifier was present, showed the presence of water in the sample drops at time of deposit. On the sampling surface a ring of different colour intensity around the stain, reproducible in the laboratory, suggests that water was absorbed into the drops during their descent through the moist atmosphere. Emulsions might be safely used where humidities are high enough to minimize evaporation.

The now commonly used oil solutions have proven best and to a large degree, effective, but nonetheless subject to change through the evaporation of their volatile fractions. These changes introduce several implications of interest.

Of the many methods of assessing spray deposit none specifically considers the effects of drop shrinkage through evaporation. Most methods measure droplets as stains, craters or lenses trapped for examination, counting, and measuring. These techniques measure drops impinged on the target after settling through varying distances and times. Extrapolating from Brooks (1947), a  $100\mu$  drop of water would require 1.8 minutes to fall 100 feet. Falling speeds vary directly as the drop size and the same source of information shows a  $200\mu$  drop falling 100 feet in 0.7 minutes, assuming no evaporation loss. A drop of oil of 0.9 specific gravity would fall more slowly. However evaporation reduces the size of the drop, thus reducing the speed of descent.

An approach to a measurement of evaporation loss has been made in which drops of known size were deposited on oleophobe-treated glass slides and weighed at intervals to determine the rate of weight loss. Further observation on drops trapped on glass filaments to maintain a nearly spherical form, in which drops were measured under a microscope, showed rapid initial evaporation which diminished as the more volatile fractions of the solution were lost to the atmosphere. The drops for both series of observations were applied using the applicator described by Rayner and Haliburton (1955). The rate of weight or volume loss (Fig. 1) was very rapid during the early period of exposure, a  $113\mu$  drop shrinking to 50% of its original volume in 6 minutes. At this point, the drop would be approximately  $90\mu$  in diameter and, if free, the rate of fall would be reduced by about one-quarter, to 2.2 minutes per hundred feet. These fall rates are based on the heavier water drops, and thus the rate of fall for the oil drops would be somewhat less. Furthermore, the fall rates were computed for drops settling in still air, a condition rarely encountered in outdoor spraying. Convection and eddying, due to air mass movement or the passage of the plane, result in a further delay in the settling of the spray cloud. Field observations have shown that the smaller drops may settle into the forest 5 to 10 minutes after the passage of the aircraft.

The single drop size used for illustration ( $113\mu$ ) represents approximately the 50% point of drop number distribution in a series of trials (Hurtig *et al.*, 1953) and therefore has some basis in fact. Since rate of fall varies exponentially with drop size it is readily seen that the drop size components of the spray cloud settle at vastly different rates and the drop samples secured on sampling surfaces represent particles which have widely differing evaporation rates. For example, to take the rates for the two significant extremes of drop sizes encountered in Hurtig *et al.* (1953), a  $38\mu$  drop would fall 100 feet in about 14 minutes while a  $380\mu$  drop would fall 100 feet in about 20 seconds. The falling times are of course subject to adjustment since the drops were measured at the time of reaching the target; the smaller drops having been several times as large at point of emission and the larger drops a fraction larger.

The above illustration shows how evaporation may change the make-up of the spray cloud during the time of descent. The investigational work to date suffices only to define the problem. Further work is designed to provide methods by which deposit analysis will result in a more precise measure of insecticide reaching the target in aircraft spray operations, taking account of evaporation and hence of increased concentration after descent.

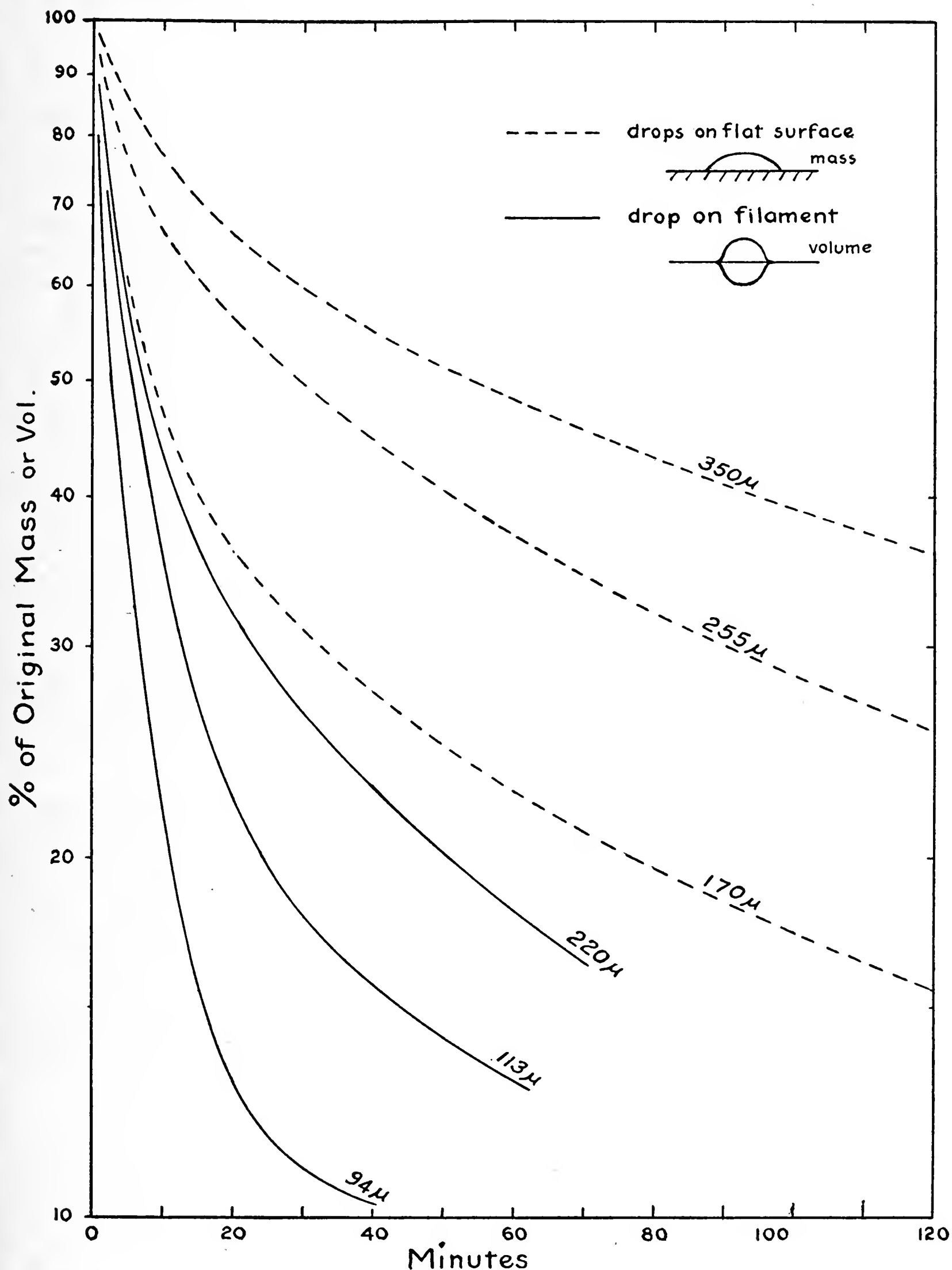


Fig. 1. Evaporation curves for exposed drops of known size. (10% DDT, 20% Velsicol AR50, 69.5% #2 Fuel oil, 0.5% Oil Red Dye.) (After Hopewell, W. W. 1956. Unpublished data, Chemical Control Section, Forest Biol. Div.)

The sampling methods now in use, particularly those which employ colorimetric analysis of dyed deposit (Hurtig *et al.*, 1953; Rayner, 1956; Yuill *et al.*, 1948; and others) give good results for insecticide measurement under favourable conditions, i.e. where samples can be gathered quickly and are not exposed to direct sunlight; but fading of the dye often introduces errors of unacceptable magnitude when used in forest spray assessment. In one trial (Hurtig *et al.*, 1953), where colorimetric analysis



was deemed acceptable for most of the samples, the dyed deposit in one plot sprayed just before a period of strong sunlight, faded almost completely in the samples which were exposed longest.

Colorimetric analysis fails to reveal important information on particle sizes and distribution, and comparison with drop spectra data has not shown the methods to be sensitive enough to bring out differences due to evaporation.

Practically all of the recent forest insect spray operations on the American continent have employed a 10% DDT solution (1 lb. DDT/Imperial gallon) or a 12½% DDT solution (1 lb. DDT/U.S. gallon.) These solutions were usually applied at the approximate rate of 1 gallon per acre or ½ gallon per acre. The application rate is determined by combining airplane speed and height with delivery rate and spray cloud drift. In one series (Elliott, 1952) the average deposit was assessed at 0.38 gpa based on ocular examination by comparison with standard cards; and in another series (Hurtig *et al.*, 1953) at 0.27 gpa based on careful analysis of stains on cards and a colorimetric analysis. In both cases the emission rate and swath width were designed for 1 gallon of insecticide formulation per acre. The obvious conclusion is that ⅔ to ¾ of the spray was lost between emission and deposition. It has been shown that evaporation during descent can be considerable, particularly of the smaller drop sizes. Much of the indicated spray loss is probably the direct or indirect result of evaporation. The analysis of drop spectra data (Hurtig *et al.*, 1953) showed deposit of drops ranging in diameter from about 25 $\mu$  to 500 $\mu$ . Recent observations also showed that drops below 50 $\mu$  in size are greatly influenced by the slightest air movements. The 50 $\mu$  drop would fall at the rate of about 14 feet per minute initially, and shrink to 50% of original weight in less than two minutes. It can be seen, then, that few of the drops 50 $\mu$  in diameter or less would reach the target, unless through the action of a downdraft of air. The smaller drops appearing on the sampling surface must have been, initially, large enough to fall through gently eddying air. Thus, great numbers of insecticide particles are lost due to diminishing size and extensive drift.

### TOXICOLOGICAL IMPLICATIONS OF EVAPORATION

Attendant on evaporation weight loss is an increase in insecticide concentration, particularly with a stable compound such as DDT. A drop originally 113 $\mu$  in diameter evaporating to 50% of its volume by the time of contact would of course have double the original insecticide concentration. Concentration increase would vary inversely with initial drop size.

Laboratory tests with formulations to be used in aircraft (10% DDT in aromatic solvent and fuel oil) have shown the ultimate instar of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Rayner and Hurtig, 1953) and the black-headed budworm, *Acleris variana* (Fern.) to be most tolerant of DDT when applied topically, requiring the equivalent of several times the recommended dose of 1 lb. DDT in 1 gallon of solution per acre to effect an acceptable kill. Field trials subsequently failed to show higher survival of late stage larvae, but rather indicated a high degree of effectiveness against all larval stages. These results raise doubts about our present concepts on dosage, spray break-up, and the nature of the desired contamination.

The evidence that topical application of 10% DDT is not effective suggests a number of possibilities: (a) that the DDT acts as a stomach poison, or must contact certain under parts of the larvae to be effective; (b) that fumes or minute drops are irritating to the larvae, causing them to become active and pick up a lethal dose in their movements, or to wriggle out of the feeding sites and fall to the forest floor where they are lost to the population; or (c) that the evaporation results in a concentration of DDT considerably in excess of 10%. The tolerance to DDT shown by these insects suggests that some other insecticide may be more effective. It is imperative, therefore, that a systematic toxicological testing program be carried out for the important forest insect pests, in order to determine the action by which an insecticide is effective and the concentrations necessary for success.

Dosages are habitually represented in gallons of formulation per acre. Experimental data usually include information on drop size spectra and the number of particles per unit area. Where all such information is available, logical conclusions may be

drawn. The statistics on gallons per acre, unsupported, are quite unrealistic and no useful inferences about spray distribution are possible. Heavy dosages in gallons per acre may represent small numbers of large drops and, therefore, result in very inefficient coverage. The reverse may also be true. Gallons-per-acre data may only be useful when the aircraft spray system has been calibrated and there is some assurance that the breakup and coverage are adequate.

Hurtig *et al.* (1953) reported analyses to determine which measurement was correlated with insect mortality, in this instance the spruce budworm. Of the numerous measurements made (gallons per acre, drop size spectra, colorimetric reading for volume, and particles per unit area) only one showed any correlation with mortality and that was quite strong. The density of particles per unit area, regardless of size (within the range of sizes encountered viz. 20 to 500 $\mu$  in diameter) showed a strong correlation with mortality measured in the field (Fig. 2). The LD 50 was located at

### RELATION BETWEEN DROPS/UNIT AREA AND MORTALITY

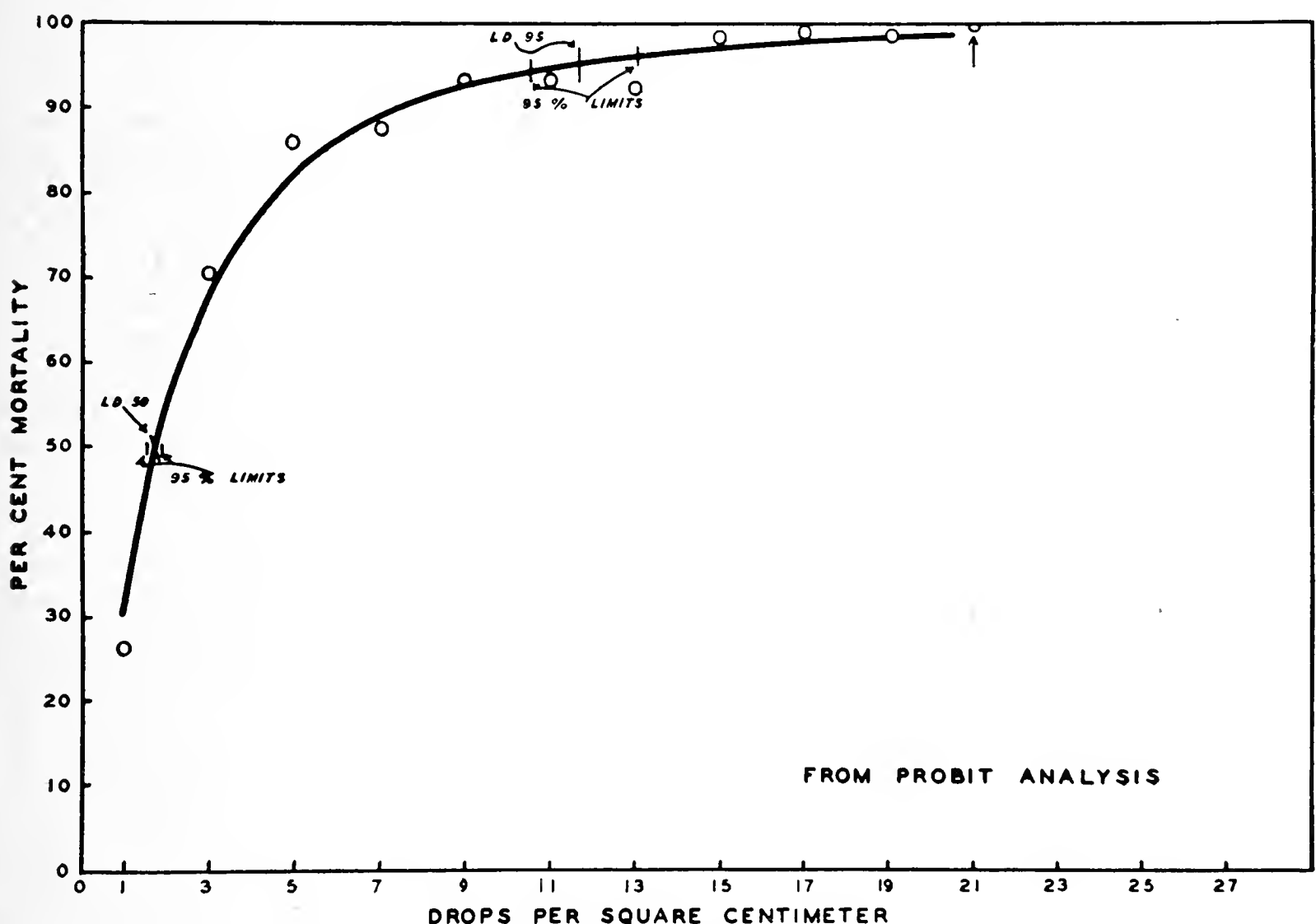


Fig. 2. Results of 10% DDT in oil sprayed by aircraft against the spruce budworm. From Hurtig *et al.* (1953).

2 drops per square centimetre and the LD 95 at 12 drops. All deposits above 21 drops per square centimetre resulted in 100% mortality. This analysis suggests that the most efficient spray is one which produces the largest number of drops which will fall, and the aim of equipment development should be to narrow the drop spectrum to produce these drop sizes. Since the drops sampled had been subjected to evaporation during descent it is not possible to define which sizes are desirable, but it is suggested that emitted drops in an approximate range from 75 to 400 $\mu$  would be quite efficient, allowing adequate differential drift to give a wide swath width. This, in effect, would eliminate the very small drops which do not deposit and the very large drops which are wasteful of volume. Uniformity of drops in the spray cloud would not be desirable because all particles of such a cloud would tend to follow the same trajectory from the flight line and therefore to narrow the swath width. A relatively wide size spectrum is needed to take advantage of wind drift and thus maintain a wide swath.

Since one result of evaporation is increase of insecticide concentration, an aim of toxicological studies should be to determine the level of final concentration needed for

a particular insect. The initial 10 or 12½% DDT is obviously deposited at a concentration considerably more than that which was emitted by the aircraft. It is probable also that the final concentration is greater than that needed to be effective. If the original insecticide content could be decreased without decreasing effectiveness, then formulation would be simpler and more economical. Samples of fuel oil #2 will dissolve 5 to 8% by weight of DDT. If similar initial concentration were found to be effective, DDT in fuel oil alone would suffice and eliminate special solvents. Some work has been done with high-boil-point gas oils which compare in price with fuel oils but dissolve up to 18% DDT by weight and have lower vapour pressures. The comparison of these oils with fuel oil is in progress and the results to date have been promising.

### SAMPLING SURFACES

The assessment of an insecticide deposit must entail the catching of the descending drops or particles on a sampling surface. All manner of surfaces have been used; glass plates, metal plates (Yuill *et al.*, 1948), slides coated with material in which oil drops maintain a spherical shape (Hurtig and Perry, 1950), Petri dishes, oleophobe coated slides (May, 1945), magnesium oxide coated slides (May, 1950), dyed Printflex<sup>2</sup> (Davis and Elliott, 1953; Elliott, 1952), undyed Printflex paper using dyed spray (Hurtig *et al.*, 1953), and filter paper (Rayner, 1956), to name but a few. The most satisfactory medium for field sampling, where drop size measurements are required, is the easily-handled paper sampling surface. Since the work of Davis and Elliott (1953), the highly uniform 'Printflex' paper has become widely used as a sampling surface for both experimental and commercial spray deposit sampling. This paper, coloured with oil soluble dye, is used for ocular estimations of deposits in large operations, where the oil drops produce stains which are related to the drops in size. For experimental use the paper is untreated, but the dye tracer is carried in the spray solution. Although the original users suggested that the ratio of drop diameter to stain diameter for dyed paper was fairly constant at 1:6 to 1:7, depending on the solution, careful examination using newly developed apparatus for producing uniform drops (Rayner and Haliburton, 1955; Rayner and Hurtig, 1954), showed that the stain size varied with drop size over a wider range. In the work by Hurtig *et al.* (1956) a calibration curve showed a spread factor range from 3.6 to 6.7 for a drop size range from 60 $\mu$  to 500 $\mu$  in diameter. These spread factor values were lower by about 10% for dyed paper.

Recently, Printflex paper was calibrated for spread factor for several insecticidal and standard solutions. The results were quite similar to those of Hurtig *et al.* (1956) but the calibration curves (Fig. 3) show a steeper slope. Furthermore, each formulation has a characteristic spread factor curve, which, while related in slope and shape, differs in height. The curves for 5% BHC, and for 10% DDT in high aromatic solvent, have steeper slopes than the others. It is suspected that the presence of an emulsifier in the original concentrates is the cause. The curve for dyed water is perfectly horizontal throughout the full scale of drop sizes. May's data (1950) for MgO-coated slides show an inverse ratio of crater size to drop size with a sharp rise for the smallest size measured.

The foregoing points up the need for careful calibration of any surface to be used for deposit assessment where drop sizes are to be measured. The standard curve for each formulation must be determined and the characteristic spread factor for each size class must be employed in the computations. Since a 3% error in drop diameter represents an error of about 10% in volume, use of an inaccurate spread factor could be seriously misleading.

### METEOROLOGICAL ASPECTS

One of the keys to effective forest insect spraying by aircraft is that of meteorological conditions at the time of spray emission. The spray cloud is almost entirely under the influence of air currents, both of mass movement and of turbulence. Much has been written on the subject of the effects of wind, turbulence, temperature gradient and drift (Bleasdale, 1942; Brooks, 1947; Brown, 1951; Chamberlin and Getzendaner, 1955; Gunn, 1948; Ripper, 1955; and others) but little has been reported relating these findings to the peculiarities of air movement in and around forested areas. While

<sup>2</sup> A filled, sized and callendered printers' cover stock. Mead Paper Corp., Chilcothe, Ohio.

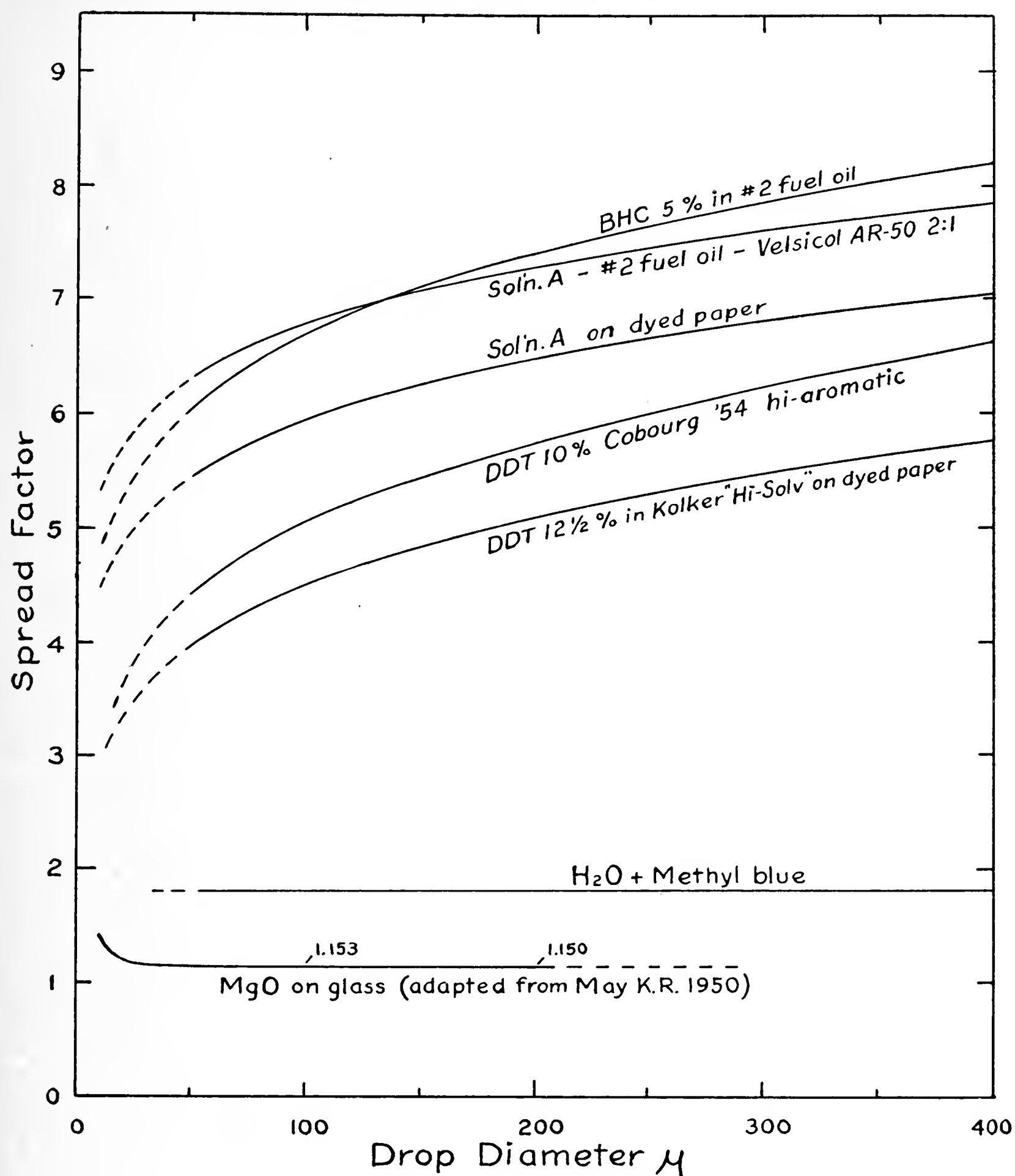


Fig. 3. Spread of oil solutions on Printflex paper. (After Haliburton, W. 1956. Unpublished data, Chemical Control Section, Forest Biol. Div.)

the principles involved must pertain to forests as well as open ground, the application of these principles to forest spraying may require adjustment.

The Porton method of drift spraying (Gunn, 1948), in which wind speed and plane height are combined to produce uniform drift for varying conditions, is ideal for experimental spraying but difficult of application in remote areas where meteorological measurement cannot be obtained. Use of knowledge of air currents over areas to be sprayed would result in more uniform coverage and possibly an extension of the meteorological conditions under which spraying is now considered feasible. Many of the air turbulence conditions which cause non-uniform deposit in crop spraying (Chamberlin and Getzendaner, 1955) are of minor concern in forest spraying. The greater spray height tends to even out the effects of turbulence and deposit gaps peculiar to low level flying.

The method of measuring temperature gradient to indicate turbulence and air mass stability (Bleasdale, 1942) has been employed in several operations (Hurtig *et al.*, 1953), but the method was developed over open ground. Geiger (1950) has shown that temperature inversion persists in the forest for some time after lapse has occurred in nearby open fields. Personal observation has shown that lapse conditions strong enough to force termination of spraying, measured in an open site 50 yards from the forest, occurred when inversion continued in the forest. It is possible that forest spraying could be carried on under conditions which would be too turbulent for open country application. Over grass, the wind may drop from strong to light within a few inches while in the forest a similar drop would occur over 15 feet or more (Geiger, 1950). Furthermore, the forest canopy does not present the solid barrier to spray settling and downdrift that is present near the ground, as in crop spraying. Therefore the presence of inversion within the forest and the lack of a barrier suggests that spraying may be done over forests for longer periods than is now deemed advisable.

The foregoing, while somewhat conjectural, is presented to point up the necessity for investigating the meteorological aspects of spraying, related to insecticide deposit in a forest environment. The results of many studies of these factors for open ground conditions should facilitate such investigations.

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## DISCUSSION

J. S. YUILL. You find that topical application of DDT is not highly effective on spruce budworm larvae. Do you believe the fall of larvae immediately after spraying is due to irritation caused by the fuel oil or some fumigant effect?



J. J. FETTES. I believe that is true, although increased insecticide concentration may also be a factor in larval mortality.

G. PAQUET. I would like to ask Dr. Fettes what he thinks of the reliability of dyed assessment cards and of the advisability of using them to ascertain if an area has been properly sprayed.

J. J. FETTES. When used properly, the dyed cards are quite reliable. They must be carefully put out in forest openings a short period before spraying and picked up soon after. The cards are not reliable where the drops are less than  $90\mu$  in size. If it is desirable to check spray application beyond that of check planes and pilot reports, cards should be used.

G. PAQUET. I understand that in New Brunswick for the last two or three years they have not been using dyed assessment cards. Is it because they do not rely on them or because it requires too much field work to deposit them and to pick them up after spraying?

J. J. FETTES. Partly both. Some mortality has been noted where cards have been negative and the vast physical problem of using cards over great areas have discouraged the use of assessment cards.

R. E. BALCH. Is there not a weakness in the failure of the dyed cards to record the very small droplets which may form an important part of the spray cloud? What is the minimum size recorded?

J. J. FETTES. Yes, since there is a minimum size of drops which will show on a dyed card it would be possible to apply a lethal dose which would not be visible on a card sample. This situation would be rather rare. The lower limit of drop size visible on a dyed card is about  $80\text{--}90\mu$ .

J. S. YUILL. In the United States cards are used as an indicator rather than a positive evaluation; that is, if deposit is considered marginal, foliage and budworm larvae are examined for evidence of spray coverage.

D. E. PARKER. In aerial spraying in Montana and Idaho, dyed cards are used. They have a psychological effect on pilots. Checkers noting cards with little or no spray check drop of larvae in surrounding area for spray effect. Observation planes during spraying, dyed cards, and insect checkers are necessary for good operations.



# Spruce Budworm Control in Oregon and Washington, 1949-1956<sup>1</sup>

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## ABSTRACT

The spruce budworm has been known in Oregon and Washington since 1914. The first major epidemic started in 1944 and is still in progress. An effective control method was unknown until 1948, when co-operative experiments obtained upward of 95 per cent control by proper timing of aerial spraying with one pound of DDT in one gallon of solvent and fuel oil, applied at a rate of one gallon per acre. Based on these results and findings of annual, comprehensive surveys, a co-operative control program has been conducted since 1949.

During seven years' spraying the following has been achieved: Budworm mortality averaging 98.2 per cent, successful treatment of 3,840,000 acres for approximately \$1.05 per acre, co-operative financing of control, establishment of rigid contractual procedures, testing of airplanes and spraying equipment, and development of trained personnel and organizational details for safe, effective control projects. Forest values above 1 billion dollars have been saved, with severe tree mortality confined to less than 10,000 acres. Budworm populations on treated areas remain low and re-infestation is negligible.

Four studies conducted concurrently with control projects, tested reduced dosages of DDT, other insecticides, and increased spraying heights. Results indicated that one pound of DDT per acre is still most effective but spraying heights can be raised for at least one type of aircraft.

In 1955, natural control factors became highly significant. Consequently, spraying was cancelled in 1956. The 543,000-acre epidemic infestation that remains is being analyzed to determine the necessity for renewing aerial control in 1957.

## INTRODUCTION

The spruce budworm (*Choristoneura fumiferana* (Clem.)) is one of the most widely destructive forest insects in North America. Periodic outbreaks of the budworm in eastern Canada and Northeastern United States date back at least to 1807 (Packard, 1890). They have often continued for periods of 10 or more years and have resulted in tremendous timber losses. The first recorded outbreak in western North America occurred in British Columbia in 1909 (Mathers, 1932).

While epidemics of the spruce budworm raged in other portions of the continent, a unique situation existed in the states of Oregon and Washington for over a quarter of a century. From 1914 when the budworm was first recorded from Douglas-fir (*Pseudotsuga menziesii*) at Ashland, Oregon, to 1943 when the first extensive outbreak developed in northeastern Washington, only small, localized, and widely separated infestations occurred on various forests in the eastern portions of the two states. All of these outbreaks subsided from natural causes without any appreciable loss of timber. This is quite remarkable in view of the well-known destructive potential of the budworm and the vast amount of host material present in the two states.

During this period, no control measure was known and none was considered necessary. The budworm was just another insect in the extensive fir forests of Oregon and Washington.

Since 1944, the picture has changed. The spruce budworm is no longer ignored. Over \$4 million have been spent to treat 3,840,000 acres of epidemic infestations in Oregon and Washington during a seven-year period from 1949 to 1955. Wholehearted cooperative efforts have prevented extensive tree killing and have proved the practicability of aerial spraying to control this defoliator. It can be safely stated that this timely program has protected the highly important Douglas-fir industry of the Pacific Northwest from destruction by the spruce budworm.

<sup>1</sup>Also published as a miscellaneous paper by the Pacific Northwest Forest and Range Expt. Sta., November 1956.

Control operations were suspended in 1956 because the presence and abundance of natural control factors indicated that the epidemic might subside without further treatment. The budworm is being carefully watched and aerial spraying operations will be resumed if necessary.

I would like to briefly discuss the development and accomplishments of our aerial-spraying program against this destructive native insect.

### BACKGROUND

For the benefit of those not familiar with the locale of this paper, the forest resources at stake, host plants and habits of the spruce budworm, and factors influencing control decisions, a brief summation may be in order.

**FOREST RESOURCES:** The states of Oregon and Washington are located in the northwestern portion of the United States and comprise the Pacific Northwest Region of the U.S. Forest Service. This region has a total forest-land area of 54 million acres, five-sixths of which is classed as commercial forest land. After several decades of heavy utilization, the region still has some 18 million acres of old-growth sawtimber.

About 38 percent of the live sawtimber volume in the continental United States is found in the Pacific Northwest. This region furnishes more than one-quarter of all forest products consumed in the United States each year. More than one-quarter of a million people depend upon the wood-using industries of the two states for their direct livelihood. Because of these facts, control of the spruce budworm became a matter of paramount importance both locally and nationally.

The Cascade Mountain Range divides the Pacific Northwest region into two distinct forest types. Forests of the western portion are predominantly Douglas-fir (*Pseudotsuga menziesii*), with western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), and some of the true firs (*Abies*) as associated species. In the eastern portion, ponderosa pine (*Pinus ponderosa*) predominates, and lodgepole pine (*Pinus contorta*), Douglas-fir, white fir (*Abies concolor*), and western larch (*Larix occidentalis*), are other species of appreciable occurrence.

**HOST PLANTS:** In eastern North America, the budworm defoliates balsam fir and species of spruce. In western North America the budworm has caused its greatest economic damage to Douglas-fir, true firs, and Engelmann spruce. A closely related species, *Choristoneura pinus* Free, has caused severe damage to Scotch and jack pine in the Lake States. Ponderosa and lodgepole pine in western United States have been severely defoliated by a form of the budworm. Hemlock, larch, and other conifers, when associated with preferred hosts, are also partially defoliated by the budworm.

**HABITS OF THE SPRUCE BUDWORM:** The spruce budworm overwinters as a 2nd instar larva beneath bark scales, lichen, and other protective material on roughened portions of limbs and trunks of the host trees. Upon emerging from hibernation in the spring, the tiny larvae enter and mine one needle of the previous year's growth. When the buds start to swell, larvae leave the needles and enter the expanding buds where they feed on the developing foliage. During the 4th and 5th instars, two or more branch tips are tied together to form crude nests within which the larvae feed. New growth is preferred and is almost entirely consumed before older needles are eaten. After passing through 6 instars, larvae are mature and pupate in the webbed branchlets. There is considerable evidence that at elevations above 5000 feet, budworms often have a two-year life cycle. After reaching the 4th larval instar, they hibernate for a second winter and complete their development during the following year.

Two or more years of heavy defoliation are usually required before appreciable stand mortality occurs. However, the budworm often kills trees in one year when complete defoliation takes place.

**FACTORS INFLUENCING CONTROL DECISIONS:** Because the budworm is concealed for so long a period during its life cycle, direct control measures must be critically timed. Insecticides must be applied to coincide with the short period of general feeding of 4th, 5th, and 6th instar larvae preceding pupation. During this feeding period, larvae are exposed and vulnerable.

In addition to the uncertainty of scheduling control operations, other problems are:

- (1) It is difficult to determine if control measures are necessary. Many epidemics are extremely destructive. Others subside without causing appreciable damage.
- (2) Infestation cycles are usually long, indicating that one treatment may not be sufficient to bring an outbreak under control.
- (3) Stands needing treatment range widely in current value, hence the amount of money justified to protect them from destruction varies.

### CONTROL THROUGH AERIAL SPRAYING

Our present epidemic was discovered in its early stages in 1944 on the Umatilla National Forest in northeastern Oregon. Although no accurate measures of the intensity or increase of this outbreak were made from 1944 to 1946, it was evident that a balance of natural factors, which had kept this defoliator under control, had been upset. A full-fledged epidemic was in progress.

**SPRUCE BUDWORM SURVEYS:** Reliable surveys are necessary for evaluating forest pest control needs. In 1947, the need for detailed information on the extent and severity of budworm infestations led to initiation of an annual regional survey program in the Pacific Northwest. Private, state and federal agencies have willingly cooperated in this survey.

In Oregon and Washington aerial surveys (Wear and Buckhorn, 1955) to locate and map-in-place all epidemic centers of spruce budworm infestations are conducted from about July 1 to September 15. Since 1949, the entire 45 million acres of commercial forest land in the two states has been resurveyed annually by a combination of gridiron and contour flying. We use a high-wing plane of the Cessna 180 type, two trained observers, and an experienced pilot well versed in mountain flying. Most surveys are conducted 800 to 1000 feet above the tree tops. Our aerial survey findings are carefully ground checked. These checks verify the identity of the insect or cause of damage, evaluate degree of damage, and determine more accurately the infestation boundaries.

Intensive ground surveys to locate incipient budworm infestations, not detectable from the air, have also been conducted throughout the western portion of the region since 1949. Approximately 2000 plots have been examined each year by cooperating foresters. At the end of each season a detailed report of survey findings is prepared and distributed to all interested parties.

Our first surveys in 1947 revealed 907,000 acres of spruce budworm epidemic infestations in the two states (Fig. 1). In 1948, infestations were recorded on 1,446,000 acres, with sizeable outbreaks occurring for the first time in the extensive, high-value Douglas-fir forests of western Oregon. At the peak of the epidemic in 1949, some 2,276,000 acres were heavily infested, and the budworm was present in some degree in practically all fir stands of the two states.

**EXPERIMENTAL BASIS FOR AERIAL SPRAYING:** By the fall of 1947, timber owners and managers in Oregon and Washington faced a serious problem. Budworm populations had reached epidemic proportions on nearly one million acres. Much of the attacked timber was dying; some had died; and the entire Douglas-fir industry of the Pacific Northwest was seriously threatened. And, due to the peculiar habits of the budworm, no wholly dependable control method under forest conditions had yet been evolved. Something had to be done, and soon.

It is interesting to note that the first attempted spruce budworm control by spraying in western United States was in 1929 in Shoshone National Forest, Wyoming. A small experiment using lead arsenate applied with fire hoses and pumps from the ground showed that larvae could be killed in lower portions of trees when buds were fully opened. However, this method was not satisfactory under forest conditions.

The heavy budworm populations in the Pacific Northwest afforded an excellent opportunity for practical tests of the results of small-scale, direct control studies undertaken between 1945 and 1947 in Canada and the northeastern states (Brown *et al.*, 1946; Eaton *et al.*, 1948). Insecticides containing DDT, tested against light to moderate



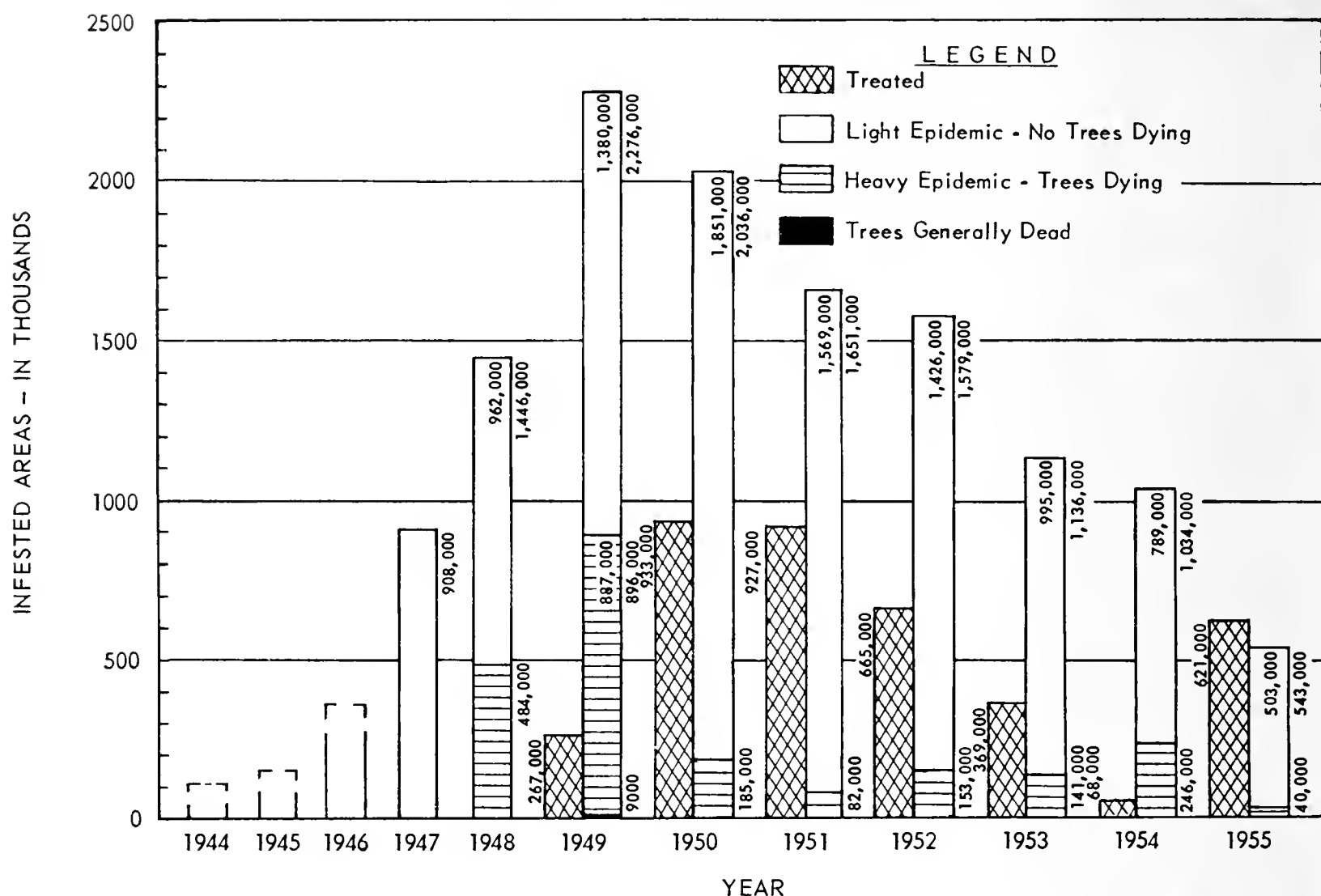


Fig. 1. Progress of spruce budworm epidemic in Oregon and Washington, 1944-1955.

budworm populations, gave promise but results were not conclusive. However, these same insecticides were very effective against the Douglas-fir tussock moth (*Hemerocampa pseudotsugata* McD.), in Idaho in 1947 (Evenden and Jost, 1947). Thus, the stage was set for a noteworthy experiment.

From May to August 1948, a large-scale, cooperative aerial spraying experiment<sup>2</sup> was undertaken against the spruce budworm in eastern Oregon to test the most promising control technique available at that time (Eaton *et al.*, 1949). Twelve 350-acre plots were treated with DDT—fuel oil solutions using dosages of  $\frac{1}{2}$ , 1, and 2 pounds of DDT per acre. Two similar plots were established as check areas. A biplane (Travelaire 4000) and a helicopter (Bell 47B-3) were used to apply the insecticides. Both were effective but the biplane was cheaper.

This experiment proved that heavy epidemic budworm populations could be successfully and economically killed by the aerial application of an insecticide containing 1 pound of DDT per acre. Upwards of 95 percent control was obtained when spraying was done during quiet morning hours and against late larval stages of the budworm when feeding on expanding foliage. For the first time, entomologists had a practical, effective, and economical method of controlling this defoliator.

It was one thing to demonstrate that the budworm would be killed by aerial spraying on a plot basis and still another to plan, finance, and conduct a full-scale control project. However, this important experiment provided the stimulus for undertaking control and developed techniques for spraying, sampling budworm populations, and evaluating control that have been closely followed during our entire program.

**SPRUCE BUDWORM ACTION COMMITTEE:** By 1948, the budworm was so widely distributed and affected so many ownerships that no one organization could control it. Federal, state and private cooperation and financing were urgently needed.

In the fall of 1948, representatives of all affected agencies, companies, and individuals met to consider survey findings and the pressing problem of spruce budworm control. A Spruce Budworm Action Committee was organized, which felt that control should be undertaken by administrative agencies existing in the two states. A control

<sup>2</sup>This experiment was undertaken near Heppner, Oregon by the former U.S. Bureau of Entomology and Plant Quarantine in cooperation with the Oregon State Board of Forestry, U.S. Forest Service, and Kinzua Pine Mills Company.

plan was prepared initiating action against centers of infestation that provided the greatest immediate threat to our timber resources. Similar meetings have been held each year and detailed control plans (N.W. For. Pest Action Comm., 1954) prepared for each annual project by this informal group, now called the NorthWest Forest Pest Action Committee.<sup>3</sup>

At its first meeting, the Committee felt that direct control should be aimed at obtaining 100 percent kill and should be undertaken only as an emergency measure to protect specific values until natural factors again suppressed the epidemic. While it might have been desirable to treat all centers of infestation immediately, technical and practical difficulties such as: shortage of time, lack of available equipment and qualified operators, and uncertain quantities of insecticides made this impractical. Therefore, priorities were established for each project in keeping with the following strategy:

- (1) to protect high-value forest of western Oregon and western Washington, regardless of infestation intensities;
- (2) to treat centers of epidemic infestation near previously controlled units, to prevent reinfestation of these units; and
- (3) to protect stands in which tree-killing is imminent within one or two years.

This strategy has been followed during our entire program. It should be mentioned in passing that in 1951 our spruce budworm problem in parts of eastern Oregon and Washington became complicated by a widespread, aggressive outbreak of the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.). Weakened by repeated budworm defoliation, tremendous numbers of trees on both sprayed and unsprayed units were killed. This situation resulted in two changes in planning budworm control:

- (1) In budworm infested stands threatened by the beetle, control was conducted sooner in the outbreak than would have otherwise been done, in order to protect the resource fully.
- (2) In budworm infested stands attacked by the beetle, further heavy expenditures for budworm control were postponed until the beetle epidemic was controlled.

At first, we did not know how many acres we could treat in one season. We needed a practical operation but not one so large that failure would be disastrous. Therefore, our first control project in 1949 covered only 267,000 acres. As a result of this experience we were able to increase the acreage treated to 933,000 acres in 1950 and 927,000 acres in 1951.

During each of our seven large-scale control projects, certain procedures have been common to each operation. While these details are numerous, you may be interested in some of the more important practices followed during the program.

**DEVELOPMENT OF OPERATIONAL METHODS:** Need for adequate research on entomological as well as operational phases of spruce budworm control was recognized early in our program. Of necessity, operational problems received most attention.

While the control projects from 1949 to 1952 were in progress we tried to improve methods by conducting one major operational experiment each year. We tested the possibility of prolonging treating periods by spraying with DDT, Benzene Hexachloride and Toxaphene against migrating 1st instar larvae to prevent one year's defoliation. These tests were unsuccessful. We studied the possibility of lowering direct control cost by using Dieldrin and Toxaphene and by reducing the amount of DDT to  $\frac{3}{4}$ ,  $\frac{1}{2}$ , or  $\frac{1}{4}$  pounds per gallon. These insecticides were applied at the rate of

<sup>3</sup>The Northwest Forest Pest Action Committee is composed of numerous private individuals and representatives of the following organizations:

Associated Forest Industries of Oregon  
Industrial Forestry Association  
Keep Oregon Green Association  
Keep Washington Green Association  
Oregon Extension Service  
Oregon Forest Fire Association  
Oregon State Board of Forestry  
Oregon State College  
Southern Oregon Conservation and Tree Farm Association  
State College of Washington  
Tree Farm Management Service

U.S. Bureau of Land Management  
U.S. Forest Service  
U.S. Office of Indian Affairs  
U.S. Soil Conservation Service  
University of Washington  
Washington Forest Fire Association  
Washington State Division of Forestry  
Washington State Forestry Conference  
Western Forest Industries Association  
Western Forestry and Conservation Association  
Western Pine Association

1 gallon per acre. The results showed that insecticides containing less than one pound of DDT per acre or containing other chemicals, gave unsatisfactory control on a unit or project basis (Brockman and Berry, 1950; Buckhorn and Berry, 1953).

We also tested the application of insecticide on a large control unit from heights above those prescribed for previous projects (Davis, 1953). The relative effectiveness of a Martin TBM at 100 and 400 feet above the treetops was investigated in interest of pilot safety. The results showed that, with this particular plane, control was just as effective at 400 feet as at 100 feet. Before raising the spraying heights for other types of planes, additional tests must be conducted.

**SAFETY:** Safety was stressed throughout. The hazards inherent in this work required detailed analysis and precise action plans covering aerial and ground operations on each project. Contracts included many provisions to safeguard all phases of control operations. These provisions were the results of recommendations based on the experience of the administrative agencies involved, the aerial-spraying industry, and the Civil Aeronautics Administration. All personnel were instructed in safety and frequent informal safety meetings were held at each airstrip during operations.

Our first project in 1949 was accident free. During the control work of 1950, 1951 and 1952 there were 10 pilot fatalities which marred our success in controlling the budworm and saving our forest resources. Since 1952 there have been no fatalities and only one serious accident.

Each accident was thoroughly investigated and reported so that similar occurrences could be avoided on subsequent projects. Safety clauses in the contracts were strengthened and strictly enforced. Rigid specifications covering pilot experience and training were prepared. As a result, a more desirable safety record has been achieved on these hazardous undertakings.

**PROJECT FINANCING:** Money to conduct these control projects was, of course, a major requirement. In accordance with the Insect Pest Control Acts of Oregon and Washington, State Foresters declared zones of infestation that included units proposed for treatment. Thus, all timberland owners within the zones were required to pay a portion of control costs. The two State Legislatures approved emergency appropriations for their shares. Almost as soon as control plans were announced, large private companies in the affected units assured their support by making financial contributions. However, since the bulk of infested acreage was publicly owned, it was imperative that federal funds be made available and in time to adequately prepare for and conduct each project.

Federal participation was carried out under provisions of Public Law 110, known as the Forest Pest Control Act. This Act recognizes federal responsibilities in controlling forest insects on lands in all ownership classes. The intent of the Act is to stimulate cooperation between private, state, and federal agencies in conducting surveys to detect and appraise forest insect outbreaks, and in controlling them. It authorizes the Secretary of Agriculture to require contributions as a condition to federal participation in control operations on state and privately owned lands.

The 1947 Douglas-fir Tussock Moth Control Project in Idaho was the first cooperative project conducted under provisions of this act. Results were highly successful and set a pattern for larger control projects that followed.

**COST PARTICIPATION:** An equitable cost-participation formula was developed and agreed upon. This formula provided that:

- (1) public agencies pay the entire cost of treating publicly-owned lands.
- (2) private owners pay 25 percent of the cost of treating their own lands, and
- (3) 50 percent of the cost of treating private lands be borne by the state and 25 percent by the Federal Government.

In 1951 the Oregon Legislature decreed that private owners in Oregon should pay 37½ percent and the State pay 37½ percent of control costs on privately-owned lands. Otherwise, control expenditures have been apportioned by the original formula.

When administrative costs were added to those of contracted services, the cost of our projects ranged from \$0.93 to \$1.20 per acre. The seven projects have averaged \$1.05 per acre.

**PROJECT ADMINISTRATION:** Administration of all control work has been divided between the Oregon State Board of Forestry and the United States Forest Service, except in 1951 when the Washington State Division of Forestry administered a small project in that state. Normally, the State agencies administered those units containing a high percentage of private land and the Forest Service administered units containing mostly federal lands. On most units, ownerships were intermingled. Cooperative agreements between Federal Government and the two states were formulated and agreed upon each year. These agreements provided for spraying and reimbursement for treating lands of all ownerships within the units administered by each agency.

Detailed plans of operation were prepared by the administrative agencies (Jorgenson and Bowen, 1951; Oreg. St. Bd. For., 1954). These plans outlined job descriptions and the responsibilities and duties of each worker. As many as 275 men were sometimes required to properly execute all phases of a single project. Prior to the start of spraying, insecticide and gasoline storage tanks were filled, telephone and short-wave radio communication systems installed, mobile and fixed weather stations manned, field headquarters established, search and rescue squads organized, and doctors and hospitals alerted.

**AIRFIELDS:** Suitable airfields and sites for construction of airstrips were selected by administrative agencies well in advance of issuing bid invitations so that contractors could inspect them and compute costs prior to bidding. All airstrips had to be accessible to tanker trucks and close to control unit centers.

Whenever possible, either regulation airfields with paved landing strips or approved emergency landing fields were used. However, many airstrips were constructed on leased private land or publicly owned lands. Grain fields, hay fields, large rock flats, and old burns were used. Some airstrips cost as much as \$18,000 to construct. Fortunately, some of these were used for more than one year. It was necessary to remove snow from many airstrips early each spring in order for them to dry out, and be ditched and graded well in advance of spraying. As many as 15 airfields were in operation during a single year.

**BIDS FOR SERVICES AND MATERIALS:** Materials and services were obtained by competitive bidding with awards made to private concerns submitting the lowest qualified bids. To have proper control over materials and services, each agency issued three separate bids on each project for:

- (1) formulated insecticide,
- (2) transportation and storage of insecticide and pumping facilities at each airfield, and
- (3) application of the insecticide on each control unit.

Formulated insecticide was purchased ready to use. For 6 of our 7 projects the insecticide consisted of a solution containing 1 pound of technical grade DDT, dissolved in 1.2 quarts of a hydrocarbon solvent, and diluted to one gallon with fuel oil. In 1951 specifications for insecticide differed in two respects from those used in 1949 and 1950. Only 0.75 pounds of DDT was required and provisions made for the use of a solvent alone in the formula. Due to a somewhat lower insect mortality on the 1951 project, the original formula was specified for the 1952 and subsequent projects. Insecticide was applied at a rate of one gallon per acre. Costs of insecticides ranged from 32 to 69 cents per gallon, depending upon availability of DDT and other factors.

Transportation of insecticide was provided by tanker truck. Two methods were used in storing insecticide. Before airfield storage tanks were set up, the insecticide was trucked from a processing plant in Portland, Ore., to intermediate field storage tanks. When spraying started, it was trucked to airfields, either directly from Portland or from the intermediate storage tanks. Airfield tanks were promptly filled at the end of each spraying day. Costs for this service and all pumping facilities averaged 11 cents per gallon.



Application of insecticide has been by many different types of aircraft, including military training bi-planes, dive bombers, twin-engine and tri-motor cargo planes, and helicopters<sup>4</sup>. However, most of the control units have been sprayed by Stearman bi-planes powered with 450 HP motors carrying 120 to 145 gallons and by Ford tri-motor planes carrying 400 to 600 gallons. In determining the number of spray planes needed to treat a given unit, we have used the Stearman with a 450 HP motor as the base spray plane and the Stearman with a 300 HP motor as the base standby plane. One Stearman has been figured to treat 10,000 or more acres on a control unit. One Ford tri-motor has been equivalent to 3 Stearmans. One B-18 or one TBM has been equivalent to 4 Stearmans. As many as 85 single-engine planes, 8 multi-engine planes, and 25 standby planes have been used on a single project.

Generally, single-engine and Ford tri-motor planes have been used on units with rough, steep terrain and deeply dissected canyons and on units intermingled with agricultural lands. Other multi-engine planes less maneuverable than the Fords have been used on units having flatter terrain and where spraying runs of 10 or more miles were possible. Costs of contract spraying have ranged from 21 to 58 cents per acre depending on the type of plane used, ferrying distances between airfields and control units, and topographic features of the unit.

**PHOTOGRAPHS, MAPS, AND MOSAICS:** Aerial photographs and maps were indispensable. A staggering number of paired photographs at a scale of 1:20,000 were purchased from all available sources and used during this program. Early in the fall of each year, men began the tedious task of preparing them for field use. Section corners were plotted on each photograph and openings and non-infested timber types of more than 160 acres in size were outlined and deleted from the project. Then control units were divided into individual spray blocks of 1000 to 5000 acres in size, using natural boundaries which could be easily recognized by spray pilots, and spray acreage and gallons of insecticide for each block and unit were computed. Photographs also were used in negotiating final acreage figures with private timber owners since it was mandatory that each owner be contacted and a signed agreement as to exact ownership secured before spraying began.

Photographic mosaics were prepared for each control unit and greatly enlarged for field use. Aerial photographs and maps of individual spray blocks were furnished to contractors and pilots for determination of logical flight patterns for each spray block and for use during spraying operations. At the end of each day, pilots indicated portions of spray blocks treated that day on a master mosaic map at each airfield. A different color was used for each day so that spraying progress could be readily determined.

**SPRAYING OPERATIONS:** Spraying for spruce budworm control must be closely supervised. Operations normally began at official time of sunrise and continued for 3 to 6 hours until wind velocities reached 6 miles per hour, or temperatures reached 68°F. Pilots often shut themselves down before these limits were reached because of rough air. Control of spray pilots was provided by observation pilots and supervisory personnel. These men were in the air almost constantly checking them for position and checking the behavior of the insecticide. When spray patterns began to "break-up", usually as a result of rising temperatures, pilots were ordered to stop spraying.

Pilots were instructed to fly at 75 to 250 feet above the treetops. However, some latitude was allowed on units with rugged terrain, and in deeply dissected canyons. Usually, overlapping lines were flown along contours. In steep canyons cross-patterning of slopes on downhill flights completed the spraying operation. In most cases spray planes operated singly, one plane to a spray block. However, tandem spraying was also successfully used. This was done mostly as a safety measure while treating remote blocks.

Split-second timing and close teamwork by ground crews were provided at each airfield. Planes were loaded with insecticide and gasoline in the least possible time to

<sup>4</sup>The following single engine aircraft have been used: Douglas SBD, Fairchild 71, Fokker Super Universal, Grauman TBM, N-3-N, Stearman PT-17, Stinson SM7A, Travelaire 4000, Vultee BT-13, and Waco.

The following multi-engine aircraft have been used: Boeing 247, Cessna T-50, Douglas B-18, Douglas C-47, and Ford tri-motor.

Bell 47B-3 helicopters have been used to a limited extent.



permit as many flights per spraying day as possible. Emergency repairs to pumps and spray booms were quickly made to avoid loss of spraying time.

At the end of each spraying day, all planes received careful inspection by certified mechanics. These men often worked all night to have planes ready for the next day.

Spraying operations are regulated by larval development. They have begun as early as May 21 and ended as late as July 27. Most of the treating has been done in June and July, with the bulk of the acreage on a project usually being sprayed during the last 10 to 15 days of operations. On practically all projects, spraying was suspended several days after starting in order to wait for larvae to reach proper treating stages. This was necessary because development differed according to elevation and exposure, being most retarded at high elevations and on north slopes.

**TECHNICAL SUPERVISION:** Technical supervision of control work (Whiteside, 1955) was the responsibility of the Division of Forest Insect Research, Forest Service, U.S. Department of Agriculture, formerly the Bureau of Entomology and Plant Quarantine. Briefly, technical supervision included:

- (1) testing of ingredients used to formulate the insecticide,
- (2) testing of formulated insecticide for DDT content,
- (3) determining the start and sequence of spraying operations, and
- (4) determining the results of control.

The first two activities were conducted in close cooperation with chemists of the Agricultural Research Service, U.S. Department of Agriculture, at Yakima, Wash.

Long before spraying began, during actual operations, and after spraying ended, a great many biological observations were conducted. These may be grouped briefly as follows:

- (1) Determination of status of overwintering populations

An annual determination of the effects of low winter temperatures on hibernating larvae on units proposed for treatment was necessary. This was done in February and March. Samples of bark and limbs containing overwintering larvae were collected from many spots on each unit and this material placed in sealed boxes in warm, lighted rooms to force larval emergence. As much as 2½ tons of limb samples were handled during a single year. Daily collections of emerging larvae were made from each box until emergence stopped. Results obtained were used in determining the status of populations and the need for control.

- (2) Determination of the start and sequence of spraying operations

One or more control districts, each including several control units, were established for each project. A Biologist, under the supervision of the Project Entomologist, was in charge of the biological work on each district. He, in turn, was assisted by 2 to 4 Insect Checkers, depending on the size of the district.

The Checkers made daily collections of 100 larvae from spots representing low, medium, and high elevations, varying stand conditions, and varying exposures of slope. These were turned over to the Biologist who examined each collection and determined percentages of larvae in each instar by microscopic measurements, or by visual comparison with predetermined larval standards. Daily progress of budworm development was charted and predictions were made as to when spraying should begin on each spray block and unit. To determine the sequence of operations larval collections were continued until all spray blocks were released.

From 7 to 10 days notice prior to start of spraying was requested by the Project Director and the contractors. This request was made so that planes and pilots could be assembled at airfields, final checks completed on spray planes and equipment, and plans made for completion of numerous last-minute details.

"Zero hour" for each unit arrived when the highest percentage of larvae reached the 5th instar and when new foliage was at least ½-inch long. When these conditions occurred, a large percentage of the remaining larvae were in the 4th instar, with a small

percentage in the 6th, and hardly any in the 3rd. In any one place or elevational zone, budworm remained susceptible to spraying for only about 10 to 12 days.

### (3) Determination of control results

Control results were determined in several ways:

- a. by checking spray deposits on glass plates or dye-treated cards,
- b. by checking larval survival on mortality lines,
- c. by spot checks throughout the unit, and
- d. by comprehensive surveys for several years following spraying.

One or two days before spraying, employees known as Unit Spray Checkers, operating from each airfield, put four-inch square glass plates or dye-treated cards in the blocks to be sprayed. Placed along compass lines at right angles to predetermined flight lines, these plates or cards were used to check spray coverage. They were carefully examined immediately following spraying so that droplet size and uniformity of spray distribution could be determined. If several plates on a given line were untouched by spray and Biologists found little larval mortality in the immediate vicinity, contractors were required to respray that portion of the block. Fortunately, there were few instances where respraying was necessary as the pilots did outstanding jobs.

Immediately before spraying, technical personnel installed mortality lines at right angles to flight lines in blocks released for treatment. A mortality line consisted of 10 stations. These were spaced 330 feet apart if established on a compass line, and 0.2 miles apart if established along roads. To determine populations prior to spraying 10 branches, 15 inches long (2 from each of 5 trees) were clipped over a collecting cloth at each station, and all budworm larvae and pupae counted and recorded. Ten days after spraying, populations were again determined at these stations. At this time, however, the sample was doubled and 20 similar branches (4 branches from each of 5 trees) were clipped at each station and examined for surviving larvae or pupae.

During the seven year period 1949-55, a total of 307,765 budworms, (307,600 larvae and 165 pupae) were collected before spraying. After spraying, only 5,604 budworms (4,711 larvae and 893 pupae) were collected. In other words, the budworm populations were reduced by 98 percent as a result of the spray program. Mortality during the different years ranged from 96.9 to 99.2 percent. Many spray blocks showed 100 percent kill and only an occasional small block fell below the 90 percent level which was considered to be the minimum acceptable degree of control.

### STATUS OF THE SPRUCE BUDWORM AFTER 7 YEARS OF CONTROL

After 7 years of intensive control efforts, the spruce budworm picture in Oregon and Washington is fairly bright.

Major accomplishments of this important control program can be summarized as follows:

1. A total of 3,840,000 acres of the most critical areas of epidemic infestations has been successfully treated at a cost of about \$4,045,000 or approximately \$1.05 per acre.
2. The total area of completely dead timber resulting from budworm defoliations has been confined to less than 10,000 acres.
3. An epidemic that started in 1944 and reached a peak of 2,276,000 acres in 1949, has been reduced to 543,000 acres in 1955. This was the lowest acreage of epidemic infestations since 1946.
4. Epidemic infestations of the budworm have been eliminated in the western Oregon area and from the eastern slopes of the Oregon Cascade Mountains during a period when a strong tendency existed for the budworm to increase on unsprayed areas.
5. Less than 1 percent of the area treated to date has had to be resprayed because of budworm reinfestation.
6. Recovery of defoliated trees after treatment has been remarkable and has proved the program's value.

7. Valuable watersheds have been protected, and creation of an immense forest fire hazard has been averted.
8. The practicability of aerial spraying to control the budworm at a reasonable cost per acre has been fully demonstrated.

Prior to 1955 there had been local indications of the increasing effectiveness of natural control factors (Coulter, 1953). Some 33 species of primary parasites have been recovered from the budworm in Oregon and Washington. Included in this list were: 1 species from eggs, 5 species from 2nd instar larvae, 19 species from mature larvae, and 8 species from pupae. In spite of these favorable factors, the budworm has maintained a high epidemic population on unsprayed areas. On units treated since 1949, control has remained effective and reinfestation has been insignificant.

In 1955 aggregate parasitism was noticeably higher than in previous years. Of even greater significance was the recovery of the hymenopteron, *Meteorus trachynotus* Vier., from mature larvae from 3 separate areas in Oregon. Entomologists in Canada and the northeastern states feel that this species, normally rare in occurrence, is one of the primary indicators of a downward trend in budworm populations (Dowden *et al.*, 1950; Jaynes and Drooz, 1952).

The improvement in the budworm parasite complex in 1955 was most encouraging. Our 1955 surveys (Whiteside, 1955) showed a declining infestation and a reduced threat of extensive tree killing by the budworm. Because of these facts, the Action Committee recommended a suspension of aerial spraying operations in 1956. For the first time in 7 years there has been a break in our control program.

Control of the budworm in Oregon and Washington was undertaken as a stop-gap measure to protect specific values until natural factors again became fully operative. We are extremely hopeful that the significant trend in effective parasitism, observed in 1955, will continue and that our epidemic may be over.

At the present moment regional surveys and research studies are being conducted to re-appraise our spruce budworm situation. Results will be carefully evaluated and a decision made whether to resume or again suspend the aerial spraying program in 1957.

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#### DISCUSSION

J. R. BLAIS. I was interested in your statement that trees on the west coast are frequently killed by one year of defoliation. Does this mean that so called "back-feeding" (destruction of old foliage) is common on Douglas fir?

J. M. WHITESIDE. Small trees are frequently killed in one year when the budworm gets ahead of the buds and kills them. Larger trees usually require two or more years before much mortality takes place. Destruction of old foliage is quite common in areas where heavy defoliation has occurred for several years.

C. J. YOPS. Kindly state your experience pertaining to fish mortality following spray application.

J. M. WHITESIDE. In Oregon and Washington we have had only one incident of fish mortality. This was a mistake on the part of the spray pilot flying over a stream several times. Sea run cut-throat trout were killed in wholesale numbers.

C. J. YOPS. Were any special precautions taken to prevent DDT applications to streams, ponds, lakes, etc. inhabited by fish?

J. M. WHITESIDE. Precautions taken to avoid damage include: (1) special briefing of pilots on blocks of high hazard; (2) limiting spray application along stream beds forming the boundaries of two or more "spray blocks" to one pass only; (3) placing an observer with a radio near critical areas who could inform the airstrip of the pilot's behaviour, i.e. too close, too low, etc.; (4) by taking pilot over critical areas to be sure he knows boundaries; (5) by not spraying streams at low water levels — often water is taken out for irrigation and at these periods streams are low; and (6) by using small planes rather than large planes and employing good pilots.



# Biological Assessment of Aerial Forest Spraying Against Spruce Budworm in New Brunswick.

## II. A Review for the Period 1952-1956<sup>1</sup>

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### ABSTRACT

*Aerial spraying in New Brunswick was undertaken as an emergency measure in 1952 to protect the extensive and valuable pulpwood forests of northern New Brunswick from serious damage by the current spruce budworm outbreak. The paper reviews the history of chemical control measures against this insect in North America and describes the policies and assessment techniques adopted in New Brunswick. The problems discussed include the assessment of hazard for developing annual control plans, timing applications, and assessment of immediate and long-term results. Each of these is complicated by the size of the areas involved, now totalling about 6 million acres sprayed in five years.*

*Studies of immediate results show that tree mortality has been largely averted in sprayed areas but is already serious in unsprayed check areas. Although large pest population reductions are effected in the generation treated, infestation recurs quickly as the combined result of a natural increase of residual populations and by invasions of moths from surrounding areas. There is as yet, however, little evidence that natural control factors have been adversely affected but continued preservation of the food supply may be delaying outbreak collapse by removing the starvation factor. Until infestation declines, continued protection may require respraying at about 2-year intervals.*

*In addition to assessing the short-term results, continuing investigations are aimed at evaluating the potentialities of the method as an adjunct to proposed long-term control by cultural measures in forest management.*

### INTRODUCTION

The status of the spruce budworm, *Choristoneura fumiferana* (Clem.), as a destructive forest pest and the influence it exerts on the North American forest economy should require little introduction here. Published literature on this insect is already extensive and one may judge from the remarks of other contributors to these symposia that current intensive investigations of the problem, both in Canada and the United States, are achieving an outstanding measure of success in clarifying some of the less obvious aspects of spruce budworm epidemiology and in relating this to the field of forest management. I believe that particular significance should be attached to the fact that the spruce budworm problem is being discussed at these Meetings from the point of view of both the research biologist and the practicing forester. This is a welcome and proper association of concepts that may never be more vital to the satisfactory solution of a difficult and challenging forest management problem.

The magnitude of the problem of spruce budworm control can hardly fail to impress anyone who is familiar with the extent of the susceptible forest types and the spectacular nature of outbreaks. Most of the investigators who have studied the problem most intensively suggest that the greatest hope of ultimately minimizing the threat of recurring outbreak lies in a measure of forest management aimed essentially at greater diversification of age-class and stand composition. Although simple enough in concept, the implementation of such a management programme, particularly in the case of the large holdings of the pulp and paper industry, will require at least several decades before the desired results should be expected. In the meantime, the prospect of eventual success along these lines offers scant comfort to the forester who is currently preoccupied with the threat of timber losses from existing or impending outbreaks.

<sup>1</sup> Contribution No. 371, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.



Neither does there appear to be much immediate prospect of success of reducing outbreak severity through biological control involving the propagation and release of non-native parasites, predators, or pathogenic diseases. It is not surprising, therefore, that large-scale chemical control, the only practical alternative for immediate purposes, was resorted to as soon as suitable insecticides became available and application by aerial means became feasible (Balch, 1953; Balch *et al.*, 1955-56).

Some idea of progress in the technical aspects of chemical control can be gained by tracing the history of aerial applications of insecticides against spruce budworm in the last 30 years (Balch *et al.*, *op. cit.*). The first trials were made in Nova Scotia in 1927, and in Ontario in 1928, using arsenical dusts. These demonstrated the limitations of the primitive application equipment used at that time and the need for more efficacious formulations. Subsequent tests were directed, principally in the United States, toward the development of concentrated sprays less affected by the vagaries of air turbulence and more likely to adhere to the foliage. Several types of emission systems were devised to disperse liquid sprays and of these the boom and nozzle arrangement has been most widely used. It was not until DDT was commercially available in quantity, however, that large-scale operations became feasible. Following experimentation in eastern Ontario in 1944 by investigators from both Canada and the United States, control operations totalling 93,000 acres were carried out in 1945 and 1946 in the Lake Nipigon area north of Lake Superior. Subsequent studies were somewhat inconclusive with regard to the long-term benefits, but they showed that DDT was remarkably effective in temporarily reducing populations and reducing immediate hazard. The operations also proved the feasibility of conducting extensive control measures over the type of remote forested areas in which outbreaks commonly occur. In 1949 the first of a series of full-scale operations was commenced in the Douglas fir forests of Oregon and Washington and in Canada intensive experimental studies were continued in co-operation with the Defence Research Board in the Kenora area of Ontario in 1951 and 1952. The results of the latter have been summarized by Prebble (1954) based on technical reports by Hurtig and his associates (Hurtig *et al.*, 1953) and will be referred to, in part, elsewhere in this paper.

Spraying in New Brunswick was commenced in 1952, and in 1954 was extended across the provincial boundary into the Lower St. Lawrence-Gaspé region of Quebec. These operations, together with those in western United States since 1949 provide some of the most impressive statistics in forest insect control. Total acreage treated in both countries now amounts to about 15 million acres or over 23,000 square miles. Over half of this applies to operations in eastern Canada since 1952 of which over 6 million acres are in New Brunswick alone. The largest operation of any year was that of 1956 in New Brunswick and Quebec. Nearly 2½ million acres were sprayed between June 6 and July 1 at the rate of ½ lb. DDT per acre. This involved a fleet of over 100 spraying and observation aircraft operating from 14 airstrips constructed for the purpose in previous years.

The story of the organization and execution of the Canadian operations over the past five years is an interesting one that is not within the scope of this paper. This has been reviewed for the first three years in a recent article in *Forestry Abstracts* by Balch *et al.*, (1955-56) and supplementary citations are appended below. My present intention is to outline some of the problems of biological assessment that have been encountered and our efforts to solve them. While it is still too early to form conclusive opinions on long-term results, it will also be of interest to examine results to date in the light of the usefulness of the method for immediate purposes and its potentialities as a tool in forest management.

## DECISIONS RELATING TO THE DEVELOPMENT OF CONTROL PLANS

One of the decisions to be made in planning forest spraying concerns the stage in the outbreaks at which control should be applied. This will depend upon whether the objective is to suppress the infestation in the early stages or to postpone action until treatment is necessary to prevent mortality or serious damage to the forest crop with the hope that the outbreak will eventually decline from natural causes. In the case of the spruce budworm the suggestion has been made that incipient outbreaks might

be checked by chemical means if focal points could be detected and eliminated early in their development (Prebble, 1954). This presupposes, however, a degree of annual survey coverage and efficiency that is yet to be realized over much of Canada's forests and, therefore, this approach is unlikely to be practicable for some time to come. The policy generally adopted in Canada has been to delay treatment until a further year's attack would seriously threaten the life of trees. This is based on the assumption that unnecessary spraying of an outbreak already on the verge of collapse is likely to be avoided and gives natural control factors the best opportunity to exert a regulating effect. Decisions on the year to spray, therefore, must be based on (1) a knowledge of the tolerance of host trees to sustained attack and (2) some assurance that continued severe attack would otherwise occur in the season for which spraying is proposed.

Information on the rate at which balsam fir mortality might be expected to develop in a sustained outbreak was available from studies of preceding outbreaks in Ontario (Belyea, 1952). These results have since been corroborated by our studies in New Brunswick in unsprayed check areas reserved specifically for assessment purposes. In these, the first dead trees above the suppressed understory were discovered in 1954, four years after the initial severe attack, (defined as loss of at least 70% of the current foliage crop). In general, sprayed areas have been first treated 2 or 3 years after the initial severe attack. While this policy has been largely successful in delaying the appearance of serious tree mortality, it has not prevented a certain amount of leader-killing sometimes extending several feet from the tips of trees. This type of damage is still evident in New Brunswick balsam fir stands that survived the previous outbreak, which ended about 1920, from the presence of some degree of deformity in the stem at the point of damage, or in forked tops. In a stand studied on the Green River Watershed it was found that top rots had invariably entered at the deformity if the original dead tip exceeded 0.5 inches in diameter (Stillwell, 1956). Pathological studies are being continued by D. R. Redmond of this laboratory to determine the influence of both top and root rots on the ultimate economic value of affected trees and these may throw some light on whether this factor is sufficiently important to warrant earlier spraying to prevent top-killing as well as complete tree mortality. In addition to the question of rot penetration, it will also be of interest to determine whether the setback to terminal growth, coupled with subsequently improved radial growth in trees released by partial stand mortality may eventually produce stems of inferior form class to those unaffected by budworm damage.

Following 1952, the succeeding years' operations have involved treatment of new areas of high hazard as they developed in the expanding outbreak and by now have covered most of what are believed to be the highly susceptible forest types in the Province (Fig. 1). In 1953 and 1954, respraying of areas considered inadequately treated in previous year represented some 10% of each year's programme. In 1955 and 1956, however, respraying amounted to about 25% and 50% respectively, and was recommended largely owing to the necessity of providing further protection to areas in which reinfestation had resulted in a recurrence of high hazard, mainly those first treated in 1952-53. Thus the problem of assessing hazard is becoming more and more one of evaluating the ability of trees to withstand successive attacks and of judging the maximum allowable time between successive treatments to maintain adequate protection. Before discussing the results to date, however, it may be of interest to indicate briefly some of the problems encountered in appraising hazard and assessing results and to describe the techniques that have been developed to cope with these problems.

### ASSESSING HAZARD

Decisions on areas in need of treatment must be made several months in advance to provide adequate time in which to solve the many technical problems involved in large-scale operations. This requires an assessment of hazard based on a detailed knowledge of the degree of defoliation and the prospects of continued attack. Owing to the large areas involved in the New Brunswick outbreak (currently over 8 million acres) this has called for the organization of intensive surveys to obtain maximum possible amount of information from the outbreak areas within the usual limitations of available time and staff. Aerial surveys are carried out in July to obtain a preliminary

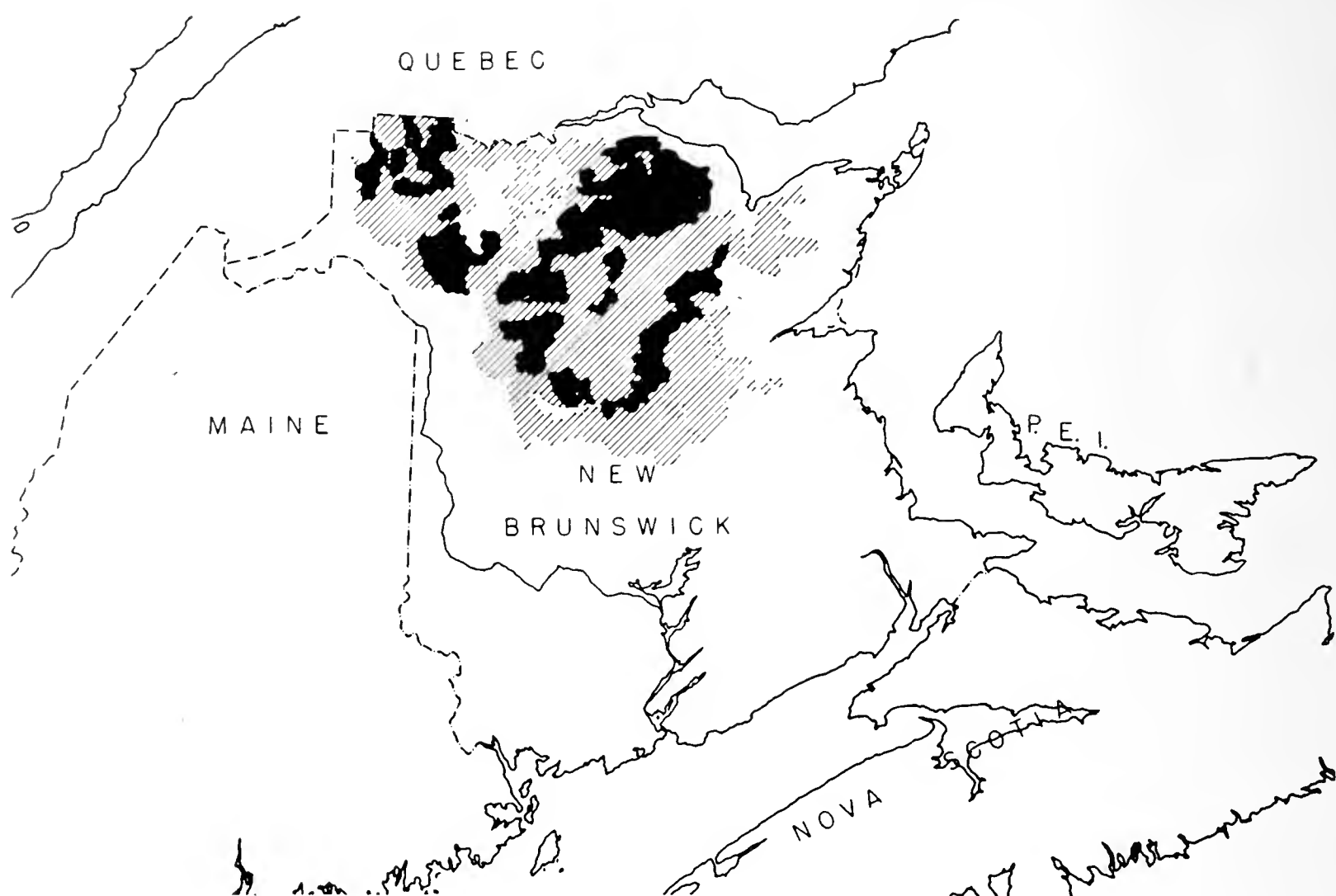


Fig. 1. Aerial spraying operations against spruce budworm in New Brunswick 1952-56. Cross-hatched areas sprayed one year only; solid areas sprayed two years or more.

appraisal of defoliation and damage and the degree of protection evident in areas newly treated (Balch *et al.*, *op. cit.*; Webb and Williams, 1956). These are supported in August and early September by ground surveys along roads and trails to obtain closer estimates of current and total defoliation, to appraise recovery in sprayed areas, and to obtain foliage samples from which to estimate egg populations of the new generation. These latter are transported to field laboratories to be examined by counting crews under proper supervision. Standard counting procedures have been worked out using a somewhat revised version of a sequential sampling technique developed for the purpose by Morris (1954). The purpose of this system is to ensure the maximum economy of sampling effort by limiting the number of counts per location to the minimum required to define population categories within given limits of statistical reliability (Webb *et al.*, 1956).

The rating of hazard from the survey data is not a simple matter because it must take into account the various combinations in which the several categories of current defoliation, total damage, recovery, and egg populations may occur. For example, the hazard represented by a given egg population in lightly-defoliated stands is less than in stands in an advanced stage of attack. Similarly, previously sprayed stands, although showing some degree of recovery, are less likely to be able to withstand recurring heavy defoliation than those approaching high hazard conditions for the first time. This problem has been solved by attributing empirically-weighted numerical values to the various assessed conditions, which when summed, represent quantitative estimates of hazard as measured at each location. When these are plotted on a map, areas in which high hazard predominates may be easily delineated and the results form the basis for control plans in the following season.

#### TIMING AND DOSAGE IN RELATION TO IMMEDIATE RESULTS

Once the control plan has been developed it is necessary to decide the stage in the insect's life cycle at which treatment is to be applied. The spruce budworm in eastern Canada is a univoltine species that feeds as a larva during May and June. During approximately the first half of this period the tiny larvae are relatively well concealed. Most commence mining in older needles and transfer later to unopened buds. Although

this feeding is relatively inconspicuous, much damage may result in heavy infestations from the killing of buds before they open. Early in June the bud-scales part and with the flaring of the new needles the larvae become more and more exposed. This stage in foliage development coincides roughly with the peak of the third instar and it is between this time and the commencement of pupation, a period usually lasting about 3 weeks, that spraying is customarily carried out. Although Hurtig and his associates have shown that ultimate-instar larvae are relatively more resistant to poisoning than earlier instars, the degree of exposure to the contact effects of the insecticide appears to be the more important factor determining the degree of population reduction effected under field conditions (Hurtig *et al.*, *op. cit.*). Thus, the best results in terms of population reduction have invariably been achieved by spraying late in the feeding period. On the other hand, sixth-instar larvae destroy several times as much foliage as all earlier instars combined, so that spraying before this stage is reached has the advantage that it is likely to provide a greater degree of protection to new shoot growth. Timing in these eastern Canadian operations since 1953 has been based on a policy of reaching the best possible compromise between these somewhat conflicting objectives. This has been described in a recent paper (Webb, 1955) and may be explained by reference to Fig. 2. This shows the alternate curves of effectiveness in terms of population reduction (upper graph) and foliage preservation (lower graph) from assessment data for the 1954 operation. Percentage kill was found to bear a more or less direct relationship to timing and reached practically 100% 3 days before the first pupation. The maximum preservation of foliage (70-75% of the current crop) was effected by spraying just prior to the peak of the fourth instar nearly two weeks earlier. The optimum treatment date, therefore, lay somewhere between these extremes depending on the relative emphasis placed on each objective.

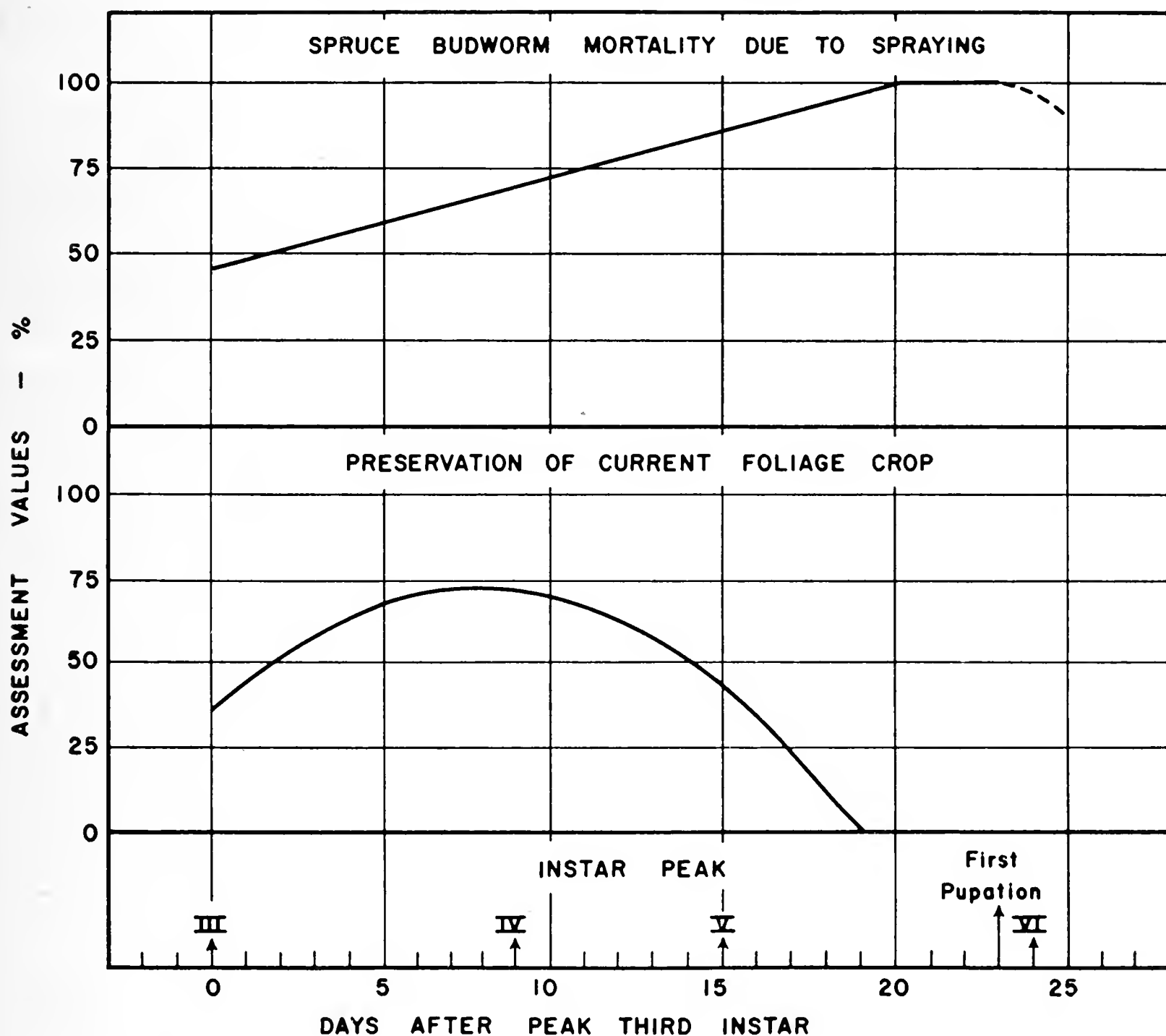


Fig. 2. Effectiveness of aerial spraying in terms of spruce budworm population reduction and preservation of current foliage — 1954 operation.



It is only in theory, of course, that timing can be arranged with the preciseness indicated in these data, since in practice, complications arise from the vagaries of weather and from phenological differences between years and within the operational area. In operations on the scale of those described here, timing must be based on a limited amount of measurement data from selected locations supported by more extensive observations over the area at large. The procedure followed during the past four years has been to obtain daily reports on insect and foliage development from representative plots and to use this basic information in judging comparative development in less accessible areas by observing phenological changes in the forest from low-flying aircraft. In particular, the peculiar light color of newly-opened shoots on balsam fir provides an indication of the earliest time at which spraying will be effective (Webb, 1955).

Advantage can be taken of differences in phenology in a large operation by deploying the spraying fleet to concentrate operations in areas of optimum development. Phenological differences of as much as 2 weeks have been observed within the areas currently under treatment. Consequently, it is possible to assign most of the fleet to the more southern bases when spraying begins and to shift later toward the north. In 1955 the New Brunswick operations, involving six operational bases, was completed in 20 days, whereas the average operational period per base was 11 days.

The decision to base timing in New Brunswick operations on a compromise between population reduction and foliage preservation is linked with that concerning the reduction in dosage from 1 to  $\frac{1}{2}$  gallon of formulation per acre. The first operation in 1952 was carried out using an emitted dose of 1 lb. DDT in 1 U.S. gallon of naphthenic solvent per acre with the objective of getting the highest possible larval mortality. The results, from this point of view, were extraordinarily satisfactory with larval mortality very nearly 100% as compared to unsprayed checks. At the same time, however, foliage preservation was poor, and reinfestation in the next generation as the result of large-scale moth invasions was much greater than anticipated. In spite of the effective larval kill, therefore, hazard remained high, indeed so high that most of the areas were resprayed the following year. In 1953, timing was altered to improve foliage preservation by commencing spraying earlier. In addition to this, cost per acre has been reduced by spraying at an emitted dose of  $\frac{1}{2}$  gallon/acre, since the 1952 assessment also showed that high per cent kill was obtained even on plots receiving very light doses. A comparison of average assessment results each year is shown in Table I. While the use of the lighter dose has undoubtedly resulted in lower per cent mortality, improved timing has resulted in the preservation of significant amounts of the current foliage crop. The expression of average results in terms of a single datum, considering population reduction and foliage protection equally important, provides a more convenient basis of comparisons for the various operations. This has been done by averaging per cent kill with per cent effectiveness in terms of foliage protection assuming these are equally important. On this basis, the best results were achieved in 1953, when approximately 25% of the total area was given two applications at

TABLE I—Operational Statistics and Summary of Results, Aerial Spraying Operations Against Spruce Budworm in New Brunswick 1952-56.

	1952	1953	1954	1955	1956
Total acres sprayed	200,000	1,800,000	1,100,000	1,100,000	2,000,000
Emitted mean dose DDT, lb./acre	1	$\frac{1}{2}$ *	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
Cost per acre (approximate)	\$3.15	\$1.40	\$1.05	.85	.80
Mean population reduction by spraying — %	99.7	96	68	83	88
Mean current foliage preserved by spraying — %	7	41	52	41	29
Mean rated effectiveness — %**	55	76	70	70	63
% Reinfestation in next generation as compared to unsprayed areas	48	42	47	15	61
Hazard rating for following season	High	Moderate	Moderate	Low	High

\*Approximately 25% of total area given two applications, two to three weeks apart. Study plots distributed accordingly.  
 \*\*Equal emphasis assumed for population reduction and foliage preservation.



$\frac{1}{2}$  gallon/acre two to three weeks apart. Operations in 1954 and 1955 using a single dose were approximately equally effective and showed a significant improvement over the initial operation in 1952 in spite of halving the theoretical dose. The effect on population levels of the next generation is also of interest. This was determined by extensive egg surveys of the outbreak at large and showed that egg populations in sprayed areas were 50 to 60% less than in surrounding unsprayed areas, except in 1955, when the difference amounted to 85%. Calculations of hazard ratings show the result. High hazard followed the 1952 operation due to the poor protection afforded by the late spraying coupled with serious reinfestation. In 1953 and 1954, hazard following treatment was moderate, primarily owing to improved foliage protection, with the result that respraying was not recommended. Relatively low reinfestation, undoubtedly reflecting a reduction in large-scale moth invasions, was chiefly responsible for the low hazard rating shown for areas sprayed in 1955.

Large-scale moth invasions of the type sometimes associated with wind and convective air mass movement have recurred to some extent each year since the spraying began, and it is mostly in respect to this phenomenon that the New Brunswick results appear to differ from those obtained in Oregon where reinfestation has apparently not posed a serious problem. It has been primarily because of this that the emphasis on timing and assessing results has been shifted in the direction of maximum reduction of hazard as a whole rather than merely to achieve the maximum possible per cent mortality of the generation in question. Some justification for this policy appears to lie in the fact that in spite of serious reinfestation, growth recovery in the year following spraying has generally been good and this improvement has usually been sufficient to prevent a recurrence of high hazard for a period of two and sometimes three years.

### TECHNIQUES OF MEASURING IMMEDIATE RESULTS

Several methods have been used in New Brunswick to measure the immediate reduction in spruce budworm populations. All are based on the principle of comparing sprayed and unsprayed conditions, so that, for practical purposes, calculations of per cent control represent mortality from spray alone and exclude natural control. The check areas selected for this purpose during the first three years, ranging in size up to some 30 square miles, have since been retained for long-term studies. They have already provided assurance that spraying has been responsible for delaying serious tree mortality in treated areas and studies will be continued to determine the eventual course of the outbreak and its ultimate effects on the unsprayed forest.

The most commonly-used population sampling methods involve periodic counts of living budworms on branches of specific dimensions selected from representative trees in sprayed and unsprayed study plots. Standard procedure for measuring immediate results in New Brunswick is now based on intensive and frequent counts on a series of permanent plots to establish population trends for the season. Post-spray sampling is extended to the area at large by measuring survival at the time of adult emergence at a larger number of additional locations selected more or less at random in sprayed and unsprayed areas. These counts are made on the basis of 18-inch branch tips selected 2 per tree from the mid-crown of sample trees which are also examined to determine the extent of defoliation and damage. The number of trees required at any one sampling point to establish population categories within given limits of precision is determined by a sequential counting procedure. At the same time the opportunity is taken to record the occurrence of other insects found on the branches, including other defoliators, parasites, predators, etc.

In some cases, branch sampling has been supported by counts of larvae dropping on cloth trays placed beneath representative trees, commenced before treatment and continued afterwards until dropping ceases. Tray counts are then compared with the number of living budworms found on the trees, which are felled for the purpose. Percentage mortality is corrected for natural control by similar sampling in unsprayed checks. The method has somewhat limited application, however, for measuring long-term population trends and does not lend itself well to extensive survey purposes.

Owing to the limited accessibility to ground parties of much of the area in question, additional reliance in immediate assessments is placed on ocular estimates of

defoliation and recovery obtained from aerial surveys carried out a week or so following the completion of spraying. The effects of the operation on the next generation are subsequently determined by means of the large-scale egg surveys described previously.

### ASSESSMENT OF LONG-TERM EFFECTS

Whereas immediate assessments are chiefly of value in determining the efficacy of the toxicant, and the effects of timing, weather and techniques of application, the complete appraisal of ultimate effects must be based on long-term studies of the whole ecosystem, preferably commenced before the treatment and continued as long as the outbreak lasts or measurable effects remain. Relatively few studies of this nature have ever been reported, and certainly no comprehensive investigation has ever been completed of operations on the scale of those currently underway against the spruce budworm. Many of the technological problems of aerial forest spraying have been or are in the process of being solved; much remains to be discovered by the forest biologist, however, if the method is always to be used wisely and its potentialities fully developed.

When aerial spraying was commenced in New Brunswick in 1952, a unique opportunity was presented to undertake long-term studies. This was because intensive studies of the spruce budworm problem in relation to forest management had been underway in the Province since 1945, before the outbreak commenced. The nature of these investigations and some tentative conclusions have already been described at these Meetings by R. F. Morris on behalf of the group of investigators comprising the Green River Project. Although the studies of aerial spraying described here do not form an integral part of the Green River investigations, the close association of the two projects has ensured the most advantageous utilization of established experimental techniques and facilities. Care has been taken, for example, to develop sampling and measurement techniques along the lines of those already in use, and to take advantage of the accumulated biological data relating to the local problem. Thus, one ultimate objective of the long-term biological studies of this project is to complement the more intensive work of the Green River Project by providing comparable data relating to the outbreak at large and to sprayed areas in particular.

The system of study plots now in use was established during the first three years, initially for the purpose of immediate assessments. Care was taken, however, to gather data suitable for long-term studies and some 19 sampling locations consisting of 5 plots each are now in use representing a variety of infestation and spraying histories. Five of these locations are located in purposely unsprayed areas, and together with the plots of the Green River Project, these provide the check data upon which assessments are based. Sample counts of budworms and associated species are made at periodic intervals throughout the season in a manner designed to provide essential life table data. These are supported by additional measurements of regulating factors and a special study is being made by D. R. Macdonald of the effects of spraying on budworm parasites. Associated with the epidemiological studies are those concerned with effects on tree growth and survival. Detailed foliage analyses are made annually on plot trees and annual growth trends are followed by means of weekly dendrometer readings and shoot measurements. Annual timber cruises are being made to determine the extent of tree mortality in sprayed and check areas and trees dying on permanent plots are being felled for analysis of annual rings and effects on terminal growth. From this it is hoped ultimately to relate infestation and protection to growth capacity, vulnerability and resistance of the various classes of trees represented.

Although the studies undertaken by this project are primarily concerned with effects on the insect complex associated with spruce budworm and on the growth and survival of the host trees, some additional investigation is being made of effects on other forms of life. Care is being taken to detect gross changes in populations of other pests such as mites or aphids (Webb *et al.*, 1956) and somewhat limited observations are being made on general insect abundance by means of flight traps (Macdonald, 1956). The effects of DDT poisoning on Atlantic salmon and fish food organisms are being studied by the Fisheries Research Board of Canada (Kerswill and Elson, 1955) and in 1956 the Division of Entomology instituted a survey of the effects on biting flies.

Limited studies were made in 1952 of the possible effects on birds and small mammals with generally negative results.

### A TENTATIVE APPRAISAL OF RESULTS

From the foregoing discussion of immediate results it is evident that some success has been achieved in delaying serious damage by spruce budworm in New Brunswick. Up to the present, however, it is also clear that the protection has been temporary and that recurring infestation throughout sprayed areas remains a serious threat to the continued survival of affected stands. The previous outbreaks in this Province lasted about 10 years and more recent ones in Ontario have persisted as long as 15 years. Whether or not this one will follow a more or less normal course toward an eventual decline will be influenced by the interactions between treatment and the density-dependent natural control factors. Parasites and predators, for example, are undoubtedly affected both directly and indirectly, although in some cases, apparently, not adversely. Perhaps the most obvious possibility is that the elimination of starvation, by preserving the food supply of the larvae, may prolong the outbreak. It is already apparent, for example, that protected stands are currently sustaining much higher populations than would have been the case if they had not been sprayed and were now in a dead or dying condition.

Some idea of population behaviour and the effects on tree growth on study plots representing various combinations of infestation and treatment is provided in Figs. 3 and 4. These show graphically from the top down: (1) population levels for a series of budworm generations measured at the egg stage, larval populations early in the following spring, and at adult emergence; (2) a history of defoliation measured in terms of per cent loss of current foliage; and (3) annual radial growth of balsam fir in the lower stem and per cent mortality by stems. Figure 3 compares a mature unsprayed plot from the Green River check area with two mature sprayed plots in the Upsalquitch areas, one sprayed once, in 1952, and the other each year from 1952 to 1955. The history of defoliation in each case is complicated by the prior occurrence of black-headed budworm, *Acleris variana* (Fern.), in 1947 and 1948 and in some areas by defoliation by both species in 1949. In the check plot (A) the new foliage crop was totally destroyed each year from 1951 to 1954 and this shortage of food contributed to relatively low survival at the end of each generation. The progressive decline that can be noted in both egg and larval populations in this period, led ultimately in 1955 to a population insufficient to consume the entire crop of scanty foliage.

The history of defoliation in the sprayed plots is similar except that complete loss of current shoots first occurred in 1950, a year earlier. In plot B, spraying in 1952 resulted in some saving of foliage and very low budworm survival. Although reinfestation in the next generation was relatively heavy, it was not sufficient to prevent a degree of continued recovery of shoot growth the following year. In the second year after spraying, however, the effect of treatment had disappeared, with infestation again complete and population levels of larvae and adults exceeding those on the check plot. The persistence of reinfestation each year is even more evident in plot C, sprayed each year since 1952.

The effects of treatment on radial growth and mortality of balsam fir are shown in the curves at the bottom of the graph. By 1955, on the check plot, average ring width had decreased by over 90% compared with the largest ring in 1949, and tree mortality, which commenced in 1954, amounted to about 20%. A progressive decline in ring width is also clear in the plot sprayed once, in this case, however, amounting to about 67%. The single treatment, however, was not sufficient to prevent tree mortality by 1954, but by 1955 this was less than in the check plot (6%). No mortality has occurred in plot C, and continued protection has apparently been responsible for a recovery in radial growth in 1954 and 1955.

The curves in Fig. 4 are similar in design except that they represent younger stands of balsam fir, composed largely of a 30- to 40-year-old age-class initially released following the previous budworm outbreak. The greater vigor of these trees is apparent from the fact that although current foliage was practically completely destroyed each

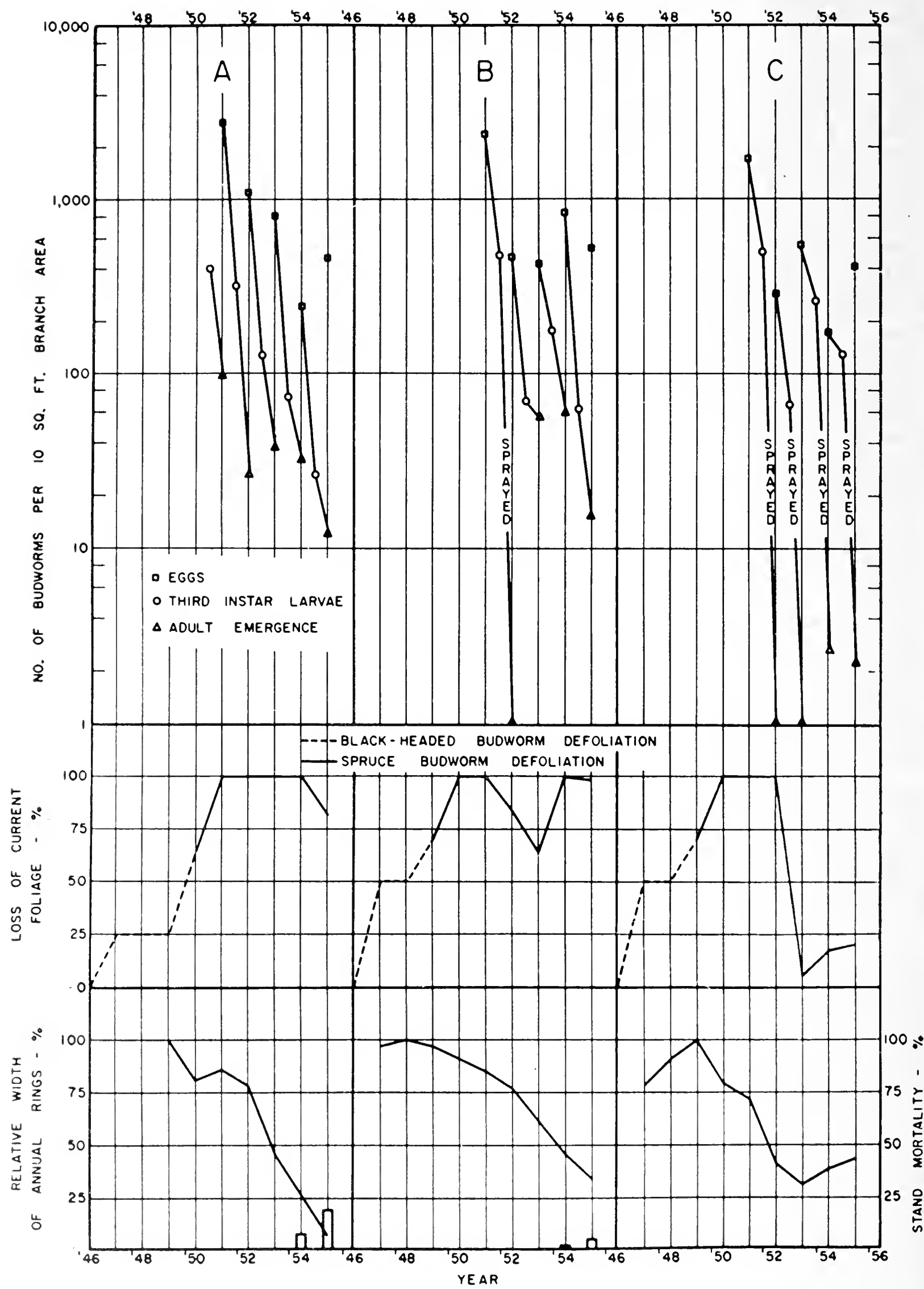
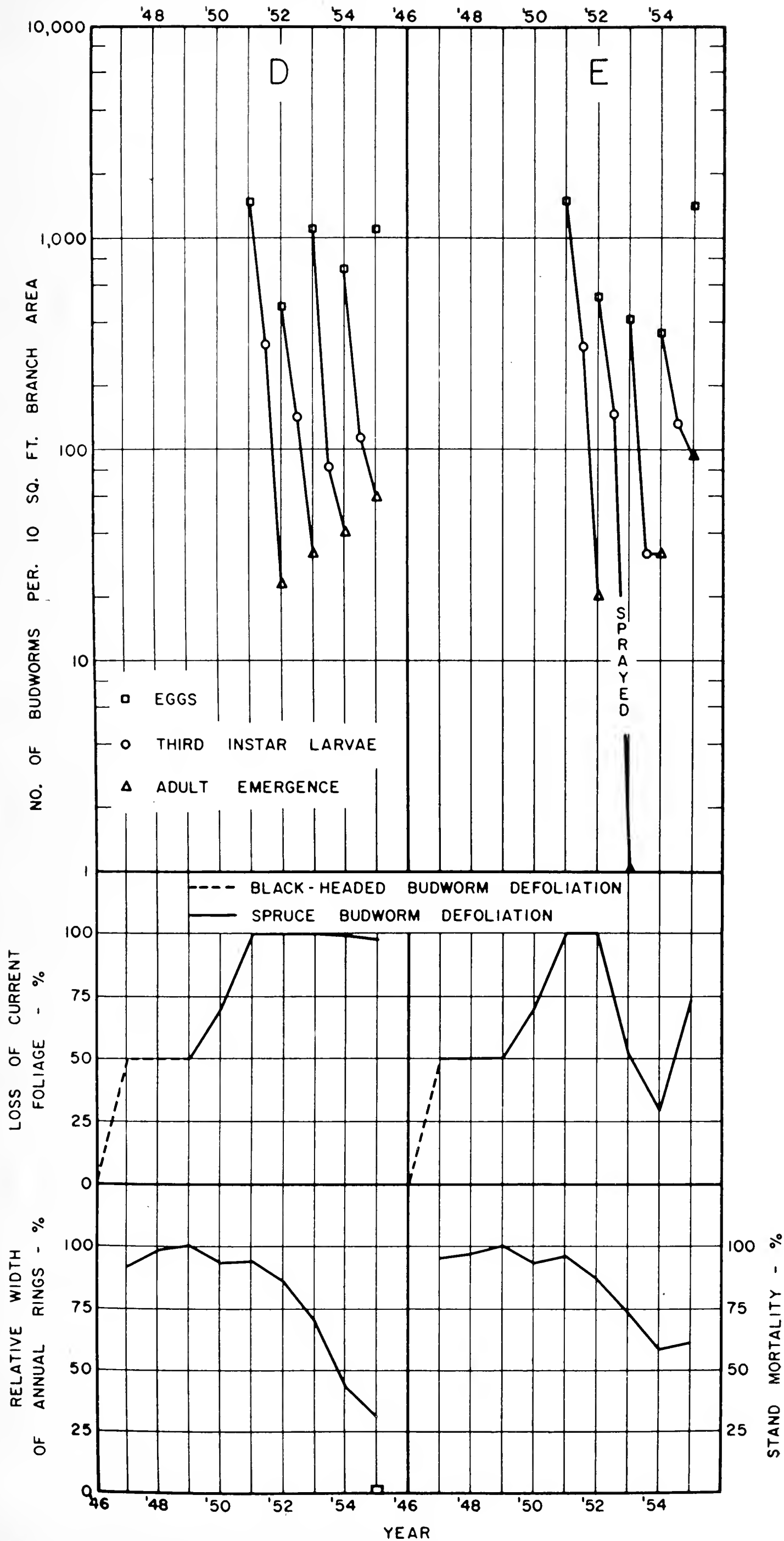


Fig. 3. Spruce budworm population trend, degree of current defoliation and balsam fir growth and mortality for representative sample plots. Plot A: Mature stand, unsprayed. Green River check area. Plot B: Mature stand, sprayed in 1952 only. Upsalquitch sprayed area. Plot C: Mature stand, sprayed each year from 1952 to 1955. Upsalquitch sprayed area.

Fig. 4. Spruce budworm population trend, degree of current defoliation and balsam fir growth and mortality for representative sample plots. Plot D: Young stand (30-40 years from release), unsprayed. Charlo check area. Plot E: Young stand (30-40 years from release), sprayed 1953 only. Charlo spray area.





year from 1951 to 1955 on the check plot D, the effects on radial growth and tree mortality are less severe than in the mature check plot A of Fig. 1. Plot E was sprayed once, in 1953, and the application was sufficiently well timed to preserve a substantial proportion of that year's foliage crop. This led to a very good recovery the following year and somewhat less than complete current defoliation and an increase in radial growth in 1955. At the same time, however, reinfestation has been as persistent as in the plots of Fig. 3, and the relatively low budworm mortality from larvae to adults is even more marked. The unusually high survival of larvae in the generation following spraying is a phenomenon that has been noted very frequently in these studies but the reasons for it are still obscure.

A consideration of the effects of spraying on natural control factors will eventually be necessary in the final analysis of the data shown in the foregoing graphs. This will involve an examination of representative life tables of a series of budworm generations subjected to various treatments. Our information to date, however, has failed to show any positive evidence that entomophagous parasites and predators have been affected to a degree likely to have a marked influence on subsequent population trends. Comparative counts of budworms, parasites, and predators found on sample branches after spraying have, in fact, shown the latter two groups to be proportionately more abundant in sprayed areas than in unsprayed areas. In 1955, for example, the ratio of parasite cocoons and puparia to surviving budworms was 1:8.3 in unsprayed areas and 1:3.3 in sprayed areas. Proportions of predators to budworms were 1:92 in unsprayed areas compared to 1:10.5 in sprayed areas (Webb, 1956). More intensive studies by D. R. Macdonald (1956) have shown that of the more important parasites, *Apanteles fumiferanae* (Vier.) in particular appears to be capable of surviving to a greater degree than the host, possibly owing to the lower vulnerability of moribund host larvae to poisoning and the ability of nearly-mature parasites to emerge and pupate from hosts affected by the spray. Whether such effects are likely to be lasting, however, depends on the host-density relationship of the parasites in question and will not be determined without further study. Continued investigation should also be made of the possibility that such favorable differential mortality between the pest and beneficial insects can be favored by suitable adjustments in timing.

A final analysis of assessment data for the 1956 operation will not be possible until this year's field surveys have been completed. Preliminary appraisals, however, indicate that rated effectiveness will be somewhat lower than in previous years, at least partly owing to the occurrence of a combination of unusual ecological circumstances. For the first time since the beginning of the outbreak, heavy flowering was general for mature balsam fir throughout the infested areas. Blais (1952) had described how such conditions favor early-instar development and survival, and Morris (1951) has shown how the phenomenon is accompanied by a temporary reduction of growth capacity and vitality of the trees. In New Brunswick, the abundance of preferred food and the ideal microclimate represented by staminate flower clusters in many stands promoted a high degree of survival and comparatively steady development of early-instar larvae in a season that has otherwise been notable for unusually delayed and erratic phenological development. This generally resulted in exceptionally rapid destruction of the reduced and retarded crop of vegetative shoots and seriously complicated the already difficult task of timing applications in a programme of record size. Added to this were the effects of spring frosts, which in many areas also killed a substantial proportion of new shoots. While such effects as these were undoubtedly of prime importance, it will be difficult to segregate them in the analysis of results from a number of other variables that may have been involved. Factors that might be suspect, for example, include the suitability of weather conditions for spraying as compared with other years, a somewhat less complete coverage of the area as a whole through the exception from treatment of many small areas of low susceptibility, and the use of a new solvent in the formulation.

Perhaps of greater importance from the long-term viewpoint is a large increase this year in the area of sprayed forest in which balsam fir is dying. In 1955 this condition was restricted to a few relatively small patches in areas of old infestation. Recent estimates of this condition for 1956 reveal that mortality ranging from slight to over 50%, and averaging 20%, occurs in sprayed areas totalling upwards of

$\frac{1}{4}$  million acres. By comparison, mortality in check areas has reached 60% in mature stands, and most of the remaining trees are beyond recovery. In younger unsprayed stands, mortality has been somewhat slower but will undoubtedly be severe within the next 2 or 3 years.

The results of 5 years of spraying may be summarized as follows. Balsam fir mortality has been substantially forestalled or delayed over an area of upwards of 4 million acres of forest while most of the trees in unsprayed check areas are now dead or dying. Under the ecological conditions that obtain for spruce budworm in eastern Canada, however, such protection is usually, if not invariably temporary, and its continuation appears to require repeated applications, using techniques described, at intervals of 2, or at the most 3 years until the stands are harvested or the outbreak declines from natural causes. Much more has yet to be learned of the ability of trees to survive prolonged attack when sprayed as frequently as every other year. The immediate problem appears to be one of mitigating the effects of the outbreak in such a way as to permit the greatest possible exploitation of existing mature stands and to preserve adequate stocking in younger stands for future harvests. The question of economic feasibility is one of deciding whether the additional cost of protection can be added to existing production costs of the industry and this must be considered in the light of the probable alternative of widespread timber losses in a region whose economy is based largely on the pulp and paper industry.

Aerial spraying against spruce budworm has already taken its place as an adjunct to short-term forest management. Its long-term potentialities are still obscure and intensive studies must be continued in the forest to determine the ultimate effects of repeated or periodic applications of insecticides on the complex biological balance. As stated previously, the greatest hope of eventual success in minimizing the threat of this insect is believed to be the development of more resistant forests by silvicultural means. There is little chance of achieving this, however, unless large areas of vulnerable forest can be protected from decimation for a period of time until the best combinations of age-class and species composition can be developed. Chemical control may be a means to this end but it must be used with discrimination and in combination with intelligent management planning. The obvious moral has been expressed by Solomon (1953) as follows: "Entomologists should do everything they can to spread the recognition that the problems of pest control are primarily ecological, and to foster the development of research and control measures which have an adequate ecological basis. In so doing they will assist the development of economic control from the empirical stage to that of a genuine science."

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# Recent Advances in Forest Entomology in India (1947-1955)

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## ABSTRACT

Serious research on forest entomology in India began in 1906 with the founding of the Forest Research Institute at Dehra Dun. The present review deals with advances made during the nine-year period (1947-55) commencing with the Independence of India. The period was characterized by considerable activity.

The biology of a large number of borers and defoliators was studied in the insectary at Dehra Dun. The field ecology of the following pests was studied: Sal heartwood borer, *Hoplocerambyx spinicornis* (Cerambycidae); Phadka grasshopper, *Hieroglyphus nigrorepletus* (Acrididae); sal and willow defoliators, *Lymantria mathura* and *L. obfuscata* respectively (Lymantriidae); *Ailanthus* defoliator, *Atteva fabriciella* (Yponomeutidae); and a number of others. The population dynamics of the Desert Locust, *Schistocerca gregaria*, was investigated.

Considerable experimental work was carried out, especially in regard to prophylactic treatments of freshly felled timber by modern insecticides, poison-girdling of trees, etc. A special feature of taxonomic work was the initiation and development of work on oriental termites. Work on the immature stages of forest insects, especially the Coleoptera and Lepidoptera, was continued. Suitable control methods were devised for a number of pests and recommendation made to the State Forest Departments, other Government departments, and private industries.

About 129 research papers, covering some 1700 pages, were published; the more important ones are listed.

## INTRODUCTION

Serious research in forest entomology in India began with the establishment, in 1906, of the Forest Research Institute at Dehra Dun. Its development is largely a record of research carried out in that Institute, although in later years a few specialised centres of research sprang up elsewhere, such as the Indian Lac Research Institute at Ranchi in Bihar (for the lac insect), the Tea Research Institute at Toklai in Assam, and the research sponsored by the Coffee Research Board in South India.

The recent advances discussed in the present paper cover the nine years' post-Independence period from 1947 to the end of 1955. In order that the recent advances may be judged against the background of earlier progress, a brief account of the early history of forest entomology in India, particularly from 1906 onward, is briefly touched upon.

## EARLY HISTORY AND PRESENT SET-UP

The early history and growth of forest entomology in India has been discussed by a number of writers, especially by Husain (1938), Rao (1938), Prashad (1939), Beeson (1941) and Roonwal (1954, for the period 1938-50).

In the 18th century, private naturalists contributed some information. Among the earliest published papers of scientific importance are the account of the life-history of an Indian termite by Koenig (1779), and the naming, description, etc. of the lac insect by Kerr (1781).

Prior to the establishment of the Forest Research Institute in 1906, some *ad hoc* zoological and entomological work was sponsored by the Government of India. In 1865, the Government directed R. Thomson to investigate timber borers; he worked in the subhimalayan regions of Garhwal and Kumaon in the Uttar Pradesh during 1866-67, and published his report in 1868. The first text-book for the use of the students of the Forest School at Dehra Dun was issued in 1888 by M. H. Clifford. In 1893 appeared E. C. Cotes' book "An Elementary Manual of Zoology Designed

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for the Use of Forest Officers in India", and in 1899, E. P. Stebbing's book "Injurious Insects of Indian Forests."

In 1900, Stebbing was appointed Forest Entomologist by the Government of India, but in 1902 the post was abolished, to be revived in 1906 when the Forest Research Institute was founded. Since 1906, entomological work has progressed steadily. The office of the Forest Entomologist (termed Forest Zoologist from 1906-21) has been held successively by the following officers:

Mr. E. P. Stebbing, 1900-02 (post abolished in 1902); Mr. E. P. Stebbing, 1906-09; Mr. V. S. Iyer, 1909-11 (temporary); Dr. A. D. Imms, 1911-13; Dr. C. F. C. Beeson, 1913-41; Mr. J. C. M. Gardner, 1941-47; Mr. A. H. Khan, 1947; Dr. N. C. Chatterjee, 1948-49 (temporary); and Dr. M. L. Roonwal, 1949-1956.

To start with, the Forest Research Institute had six research branches under the following officers: (i), Imperial Silviculturist; (ii), Imperial Superintendent of Working Plans; (iii), "an Imperial Forest Zoologist whose chief duty will be to investigate the damage caused by insects and other pests, and to suggest remedial measures" (Progr. Rept. F. R. I. for 1906-07, p. 2); (iv), Imperial Forest Botanist; (v), Imperial Forest Chemist; (vi), Imperial Forest Economist. The Institute was housed in a few bungalows in Dehra Dun town. In 1914, a new and commodious building was erected for the Institute in the Chandbagh area near Dehra Dun. In 1929 the Institute was shifted to a magnificent new building erected for it in the New Forest area about 4 miles from Dehra Dun, and here it remains. It now has 15 research branches. The Entomology Branch has extensive accommodation and comprises three main portions: (a) research laboratories, library, collections and offices, occupying the ground and first floors of the southern and eastern wing of the main building of the Institute; (b) an insectary housed in a separate building, with an attached experimental garden and a number of large field cages; and (c) two museums in the main building — a large hall serving as the entomology museum and a small one as the zoology museum. In addition, temporary field insectaries are opened in various parts of India as the need arises.

The main entomological collection<sup>2</sup> contains about 21,000 authentically identified species totalling about 200,000 individual specimens of adult insects, mainly Indian, and about 1,200 type-specimens. The collection is especially rich in the orders Isoptera, Lepidoptera, Hymenoptera and Coleoptera. The bulk of the collection is "dry" (pinned), but the Isoptera are largely in spirit (this order is represented in the collection by about 700 species). In addition, there is a large, authentically identified collection, in spirit, of the larvae of Coleoptera and Lepidoptera.

The staff consists, in 1956, of five gazetted officers, five research assistants and several field assistants, insect setters, etc.

#### RESEARCH DURING THE PERIOD 1906-46

The main items of research and related work carried out during the period 1906-46 at the Forest Research Institute, Dehra Dun, may be summed up as follows: (i) Study of the biology, life-history and ecology of a large number of forest insects, mainly Coleoptera and Lepidoptera, of India (including Pakistan), Burma and Ceylon (to a small extent); (ii), devising control measures; (iii), systematic study of forest insects, building up the collection of identified insects; (iv), maintaining ledger files for all available information of Indian forest insects; (v), building up the zoological and entomological museums.

During this period about 237 research publications were issued, mainly by Stebbing, Beeson, and Gardner. Of these, the most important ones are the large book on Coleoptera by Stebbing (1914) and the encyclopaedic book on the ecology of forest insects by Beeson (1941). Gardner (1925-48) published a large number of papers on the immature stages of forest insects.

The Indian Lac Research Institute, Ranchi, has, since its inception in 1925, done very useful work on the biology and ecology of the lac insect, *Laccifer lacca* (Kerr), and its parasites and predators. The results of this work have been summarized by Glover (1937). The tea and coffee research stations have contributed useful informa-

<sup>2</sup>A catalogue of this collection is now being issued, 21 parts having already appeared in print (Roonwal *et al.*: *Indian For. Leaf. (Ent.)*, Delhi, No. 121 (1-3), 1951-53, pp. 1-187), covering the orders Thysanura, Protura, Collembola, Orthoptera, Dermaptera, Plecoptera, Isoptera, Embioptera, Psocoptera, Anoplura (including Mallophaga), Ephemeroptera, Odonata, Thysanura and Hemiptera.



tion on the pests of these commercial plants. The Indian Agricultural Research Institute at New Delhi (formerly at Pusa in Bihar) and the Agricultural Institutes in the various States, particularly those of the Punjab (at Lyallpur, now at Ludhiana), of the Uttar Pradesh (at Kanpur), of Madras (at Coimbatore), and of Mysore (at Bangalore), have also contributed useful information on pests of certain fruit trees.

#### RECENT ADVANCES: 1947-55

The principal trend during the period 1947-55 was to intensify the experimental work on the protection of timber and the study of the taxonomy of adult insects, particularly termites. The writer, as a result of his visit to Europe, the U.S.A., and Japan (Roonwal, 1953c), assembled a large collection of about 700 species of termites at Dehra Dun. Roonwal (1954a) presented a brief review of the progress from 1938-50.

#### ECOLOGY, BIOLOGY AND EPIDEMICS

**DEFOLIATORS:** The problem of lepidopterous defoliators presents two aspects. The control of the uni-brooded defoliators (occurring in the temperate Himalayan region) is comparatively easy, for a single short operation, if successful, ensures a trouble-free period for the remainder of the year. Against *Ectropis deodarae* Prout (Geometridae), the defoliator of deodar, *Cedrus deodara*, successful control experiments, by dusting the tree trunks up to a height of about 2 metres, were carried out. This method prevents the brachypterous female moth from going up the tree to oviposit. In 1951, a serious epidemic of *Abraxas fuscescens* Butler (Geometridae), a defoliator of silver fir, *Abies pindrow*, broke out in the Lower Bashahr Division in the Western Himalayas. Exceptionally heavy snowfall next winter controlled the epidemic. The willow defoliator, *Lymantria obfuscata* Walker (Lymantriidae), was studied in 1952-53 in Kashmir.

The multi-brooded defoliators may have from 2-15 annual generations, and control, therefore, becomes difficult. *Lymantria mathura* Moore, a defoliator of sal (*Shorea robusta*) and other trees (Roonwal, 1953d), and *Atteva fabriciella* Swederus (Yponomeutidae), a defoliator of *Ailanthus* spp., are being studied. For the latter species of defoliator a temporary field insectary has been opened at Nepanagar in Madhya Pradesh.

**BORERS:** Insect borers of both living trees and of felled timber, bamboos, plywood, etc., have been studied extensively both with a view to obtaining information about the borer species affecting the various timbers, and also to find out suitable methods of control. The ecology of several borers was studied, viz., the cerambycid *Aphrodisium hardwickianum* White affecting the oak (*Quercus incana*); the cerambycid *Hoplocerambyx spinicornis* Newman, the notorious heartwood borer of sal (*Shorea robusta*) which had killed some seven million trees in 1923-28 (causing a loss of about Rs. 13,700,000 or £ 1,004,000), and had again erupted in 1949-50 (Roonwal, 1952b); and the lymexylonid *Attractocerus reversus* Walker, the borer of salai (*Boswellia serrata*), a timber potentially important for paper-manufacture; and a number of other borers.

An extensive study of the borer fauna of several species of timbers has been carried out in many parts of India (Khan, 1947; Bhatia 1950; Chatterjee, Bhasin and Bhatia 1950; Chatterjee and Chatterjee 1951). In addition, experimental work on the protection of timber, bamboos, etc., has yielded considerable information on the borer fauna; the results are now under analysis.

In the mangroves of the Sunderbans, lower Bengal, the marine borer, *Bactronophorus thoracites* (Gould) (Mollusca: Teredinidae), was found to attack living trees (Roonwal, 1954f), this being believed to be the first such record in the world.

**OTHER INSECTS:** The population dynamics of the desert locust, *Schistocerca gregaria* Forskal, was studied (Roonwal, 1947-54; Misra, Nair and Roonwal, 1952). The ecology and life-history of some species of grasshoppers (Acrididae) were studied by Katiyar (1952, 1955). The structure and physiology of the eyes and eggs of locusts was studied by Roonwal (1947, 1954d).

**PROTECTION OF TIMBER, BAMBOOS, PLYWOOD:** Soon after felling, timber and bamboos receive prompt attention from a variety of insect borers, particularly in the warmer months. In northern India where winters are severe, a short respite from borer

attack for a few months (mid-November to mid-February) is usually provided, but such is not the case in the eastern, central and southern portions of the country where the climate is more equable and almost tropical. Timber continues to receive this attention during storage in depots in the factories and subsequently in the manufacture stage as plywood, tea-chests, etc. The loss so entailed to the country is high. Consequently, considerable time has been given to the evolving of methods for the prevention of this damage. The problem has been approached from various angles, the object being to recommend those methods of insect control which are the simplest and the most economical under a given set of circumstances.

**PROTECTION BY "NATURAL" MEANS:** The degree of protection for short periods (up to about 12 months) to freshly felled logs by such simple means as debarking and by storage in the "forest-shade" or in the sun, was studied for a number of timber species. No appreciable difference was noticeable between storage in "sun" and in "shade". But debarking was found to be an effective means of preventing the attack of the heartwood borers (Cerambycidae, Lymexylonidae, etc.) and, to a certain extent, of the pinhole borers (Platypodidae and Scolytidae), because of the rapid loss of moisture in the log as a result of debarking (these pinhole borers attacking only freshly felled, moist timber). On the other hand, the gradual "curing" of felled bamboos culms, by keeping the leaves on so as to hasten the depletion of starch, did not give any marked protection against the ghoon borers, *Dinoderus* spp. (Bostrychidae).

**PROTECTION BY WATER-IMMERSION:** It is an ancient belief that immersion in water-ponds provides immunity against powder-post borers, but scientific data for Indian timbers were lacking. Experiments with three species of timbers showed that complete immersion of logs in water for a period of six months or more provides considerable though not complete immunity against borer attack in the period which follows.

**PROTECTION BY PROPHYLACTIC CHEMICALS:** Extensive experimentation, by superficially treating logs, billets, planks, and bamboo culms with several chemicals, including the modern insecticides such as DDT, benzene hexachloride (BHC), etc., showed that almost complete protection can be provided for a period of a few months to a year (Roonwal, 1951b). The most effective chemical was BHC (in a concentration of 0.5 - 1 per cent gamma isomer) in a kerosene oil medium; water-borne BHC was cheaper to use but less effective.

**PROTECTION BY PLAIN-GIRDLING AND POISON-GIRDLING:** Plain girdling, by cutting a 2 cm. deep girdle all round the trunk at a height of about 8 metres, was tried for salai, *Boswellia serrata*. Experiments on the killing of trees by poison-girdling were also carried out. The object of these experiments was to find out how far anti-borer protection is provided by these means. The results are still under study.

**PROTECTION OF PLYWOOD IN STORAGE:** Plywood panels in storage can be protected up to at least 10 months if tied up tightly in hoops and the bundle sprayed superficially on all sides with either 2-4% DDT or 0.2-0.4% BHC in kerosene (Chatterjee 1953).

General hints for timber storage under Indian conditions have been described by Roonwal (1951b).

#### SOIL INSECTS

**TERMITES:** Timber in storage is often attacked by subterranean termites (Isoptera). The damage is largely prevented if the storage-ground is first dusted or sprayed with 0.5 - 1% gamma BHC, and the stacking done on skids about 50 cm. high. More important and more complicated is the problem of termites in buildings. The problem is high-lighted by the recent case of the entire township of Shri Hargobindpur in the Punjab being in serious danger (Roonwal, 1955a). Woodwork in all the 1900 houses is infested by the termite *Heterotermes indicola* (Wasmann); nearly 400 (or 21%) houses have already fallen because of the collapse of wooden beams, and the inhabitants are gradually abandoning the town. Experimental work on a limited scale has been started with a view to finding out the best means of providing anti-termite immunity to clay-built houses.

The ecology of the mound-termite, *Odontotermes obesus* (Rambur), with special reference to population structure, has been studied by Gupta (1953a, b). In Uttar Pradesh, 17 to 27-year old trees of plantation teak, *Tectona grandis*, were found to

be so severely "debarked" by the termite, *Odontotermes parvidens* Holmg. and Holmg. in 1952, that they dried up and died (Roonwal, 1954h). Roonwal and Sen-Sarma (1955) have studied the biology of the wood-boring termite, *Neotermes gardneri* (Snyder).

**OTHER SOIL INSECTS:** The population structure of ant nests has been studied by Roonwal (1954g). Among other soil insects, the grubs of cockchafer and allied insects (Scarabaeidae, Melolonthidae, Rutelidae, etc.) damage young plants in forest nurseries. We have had no opportunity in recent years to carry out experiments on their control.

### TAXONOMIC WORK

In adult taxonomy special emphasis was laid on a revision of the oriental termites (Isoptera); the revision of the family Kalotermitidae has been proceeding apace. Some attention has also been paid to the parasitic Hymenoptera, especially the Chalcidoidea and the Ichneumonidae (S. N. Rao, 1953; Mathur, 1955).

The study of larval stages, particularly of the Coleoptera and the Lepidoptera, was carried out. A comprehensive list of the Indian Coleoptera studied so far was published by Gardner (1948) and of the Lepidoptera by Pant and Chatterjee (1950, 1951). Among the Lepidoptera, the Noctuidae were studied by Gardner (1947), the Geometridae by Singh (1953) and the Pyralidae (subfamily Pyraustinae) by Mathur (1954).

### MISCELLANEOUS ITEMS

Work was started on the preparation of a comprehensive list of insect pests of forest plants in India and the adjacent countries, the plant genera being arranged alphabetically. The first portion of this work, dealing with plant genera "A" (*Abeira* to *Azima*), has been published (Roonwal and Bhasin, 1954), and the subsequent parts are under preparation.

A phylogenetic analysis of the host plants of the lac insect, *Laccifer lacca* (Kerr) was carried out (Roonwal, 1954c), and a more comprehensive descriptive list of the host plants is now under preparation.

The establishment and dispersal of the lantana insect, *Teleonema scrupulosa* Stål, which was introduced into India from Australia in 1941, was studied (Roonwal, 1952c).

An extensive study of the food preferences of the desert locust, *Schistocerca gregaria* (Forsk.), was carried out (Husain, Mathur and Roonwal, 1949; Roonwal, 1954a). The effect of heat on the mortality of the larvae of the bookworm beetle, *Gastrallus indicus* Reitter, was studied and it was found that the minimum exposures required to kill the larvae in infested cardboards were for 2 hours at 60°C. and 1 hour at 70°C.

Some bibliographies, reviews, etc., were produced as follows: World bibliographies for the pests of teak and of bamboos were prepared for the Food and Agricultural Organization of the United Nations. A comprehensive bibliography and review of the entomological research in India for the period 1938-50 was prepared for the National Institute of Sciences of India (Roonwal, 1954a, 1954b). A list of errata of Beeson's (1941) book on the ecology of forest insects was prepared (Roonwal, 1951a), and the book itself is now under reprint.

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# Status and Trends in Forest Insect Research in the United States

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## ABSTRACT

*During the past 50 years most of the major forest insects in the United States have been identified, and much has been learned about their distribution, host preferences, and the types of injury they cause. Considerable knowledge of biologies and provisional control methods has been obtained on major species in several sections of the country. Less has been learned in other sections where demands for protection from insects have not been strong in the past. In spite of the progress that has been made, insects continue to cause huge losses annually — in 1952, they destroyed enough sawtimber to build 600,000 average size houses.*

*Good progress has been made in limited studies of biological and silvicultural control; also in studies of insect vectors of tree diseases, and in the possibilities of control through the use of systemic insecticides. Increased efforts will be made to improve on existing direct control methods; to improve on the status of knowledge of insects in regions receiving inadequate research attention in the past; to learn more about the role of biological factors in controlling infestations; to develop management practices leading to preventive control; to improve on existing survey and appraisal techniques; and to determine factors responsible for insect outbreaks and their decline.*

In discussing the status and trends of forest insect research in the United States, I shall confine my remarks largely to the work being done by the Division of Forest Insect Research of the U. S. Forest Service. In doing this, however, I trust that I will not leave the impression in the mind of anyone that I consider the work being done in several States and at certain universities, as of little or no importance. The principal reason for my decision to confine my remarks to the work of the Forest Service is that I am most familiar with it and best understand its status and trends. Another reason would be, of course, that despite the excellence of work being done by other agencies or individuals, I think that by far the greater part of forest insect research in the United States is being conducted by the Federal Government. To discuss the status and trends of its work should, therefore, go a long way towards presenting a picture of the situation in the country as a whole today.

Speaking generally, I feel that it is unfortunate that more States and institutions are not contributing to forest insect research. There is a lot of room for additional work in this field. I believe it is safe to predict that there will be an increase in this work in the next few years. It would be my guess that the trend is definitely upward. I sincerely hope so because of the rapidly expanding need for information on the control of an ever-increasing number of forest insect pests throughout the country.

Forest insect research has been underway in the United States for a long time — for more than 50 years in fact. It was as long ago as 1903 that the Federal Department of Agriculture established its Division of Forest Insect Investigations. For many years, thereafter, this work was a function of the Bureau of Entomology; later of the Bureau of Entomology and Plant Quarantine. Since 1954, it has been a function of the Forest Service. When this work began very little was known about insects which damage trees. It was quite natural, therefore, that much of the early work was involved with the identification of pest species and determination of their distribution. This in itself was hard, time-consuming work. In those days, especially in the vast coniferous stands of the West, roads were few and far between and means of transportation was correspondingly poor. Nevertheless, those early workers got the work done. In fact, it was not too long before they had pretty well catalogued the species which could rightfully be referred to as pests. During those years they also determined the host relationships of many of these pests. In fact, those early workers did their jobs so well that it has been only infrequently in recent years that we have found it



necessary to add new insect species to their list of pests, or to add new important tree species to the host lists they devised. The result is that today we feel we pretty well know what our most important pests are, where they occur, and what they feed on.

We realize at the same time, however, that conditions are subject to change. Nearly every year we learn that certain species, formerly of little importance, have suddenly emerged as economic pests. We also encounter others, long known as pests in certain regions only, which suddenly emerge in destructive numbers elsewhere. The black turpentine beetle (*Dendroctonus terebrans* (Oliv.)) in the southern part of the United States is an example of the former; the spruce budworm outbreak in widespread parts of western United States is illustrative of the latter.

Early workers in forest entomology also soon found themselves called upon to assist in the control of destructive insect outbreaks, and this is something that has continued with increasing tempo to this very day. At first, practically nothing was known of materials, methods, or equipment for use in controlling any outbreak. Therefore, considerable effort went into the development of provisional control methods. Varying degrees of success followed these endeavors and, before too many years went by, it was possible to recommend measures for alleviating damage by most species. Admittedly, many of these were crude by modern standards. This was pretty much the situation until the close of World War II.

Interest in the control of forest insects has grown rapidly in the United States during the past 10 years. Perhaps the primary stimulus was the discovery that the new chemical, DDT, could be used so successfully in such small amounts to control outbreaks of certain defoliators. By applying oil solutions of the material from the air it became possible for the first time to treat widespread forest areas for insect control. Forest Service entomologists pioneered in the development of aerial spray apparatus, in the formulation of effective dosages of spray, and in determining the effect of the sprays on fish and other forms of wildlife. Increased interest in forest insect control was engendered also by the rising value of timber and by increasing costs of control of species, such as the bark beetles, which are not subject to control by airplane spraying. A series of tremendous outbreaks of bark beetles and the spruce budworm served to point up the need for additional research on methods for preventing such calamities. Forest entomologists have long known that the only true solution to our forest insect problems lies in the development of preventive control methods, and have felt that not enough attention was being paid to fundamental studies of the causes of outbreaks. During the past few years this knowledge has begun to spread through the public's consciousness. It is perhaps safe to say, therefore, that the status and needs in forest insect research in the United States are better understood today than ever before.

Before moving on to a more detailed discussion of status and trends of forest insect research in the United States, I should like to dwell for a moment on the magnitude of the forest insect problem in the country. Possibly with this added bit of background, the items I hope to present later on will be a little more meaningful. The Forest Service has just completed a review of the Nation's timber resources with the help of a great many experts in State and private forest agencies, forest industries, conservation organizations, and other agencies of the Federal Government. A part of this huge task included the best possible estimates of insect-caused losses to the Nation's timber. I will not go into detail on the findings of this review here. I would like to point out, however, that in the year 1952 insects were found to be responsible for 28 percent of the mortality of all trees large enough to be of some commercial use in the Nation's forests. Furthermore, among the Nation's trees of sawtimber size, insects alone were responsible for 40 percent of the total mortality. The extent of this loss is hard to visualize. Some idea as to its magnitude may be gained by realizing that it included sufficient timber to construct 600,000 average size houses, or half the number built in the United States in 1954. It is to prevent or greatly reduce these losses that we are conducting our research. In the discussions of status and trends which follow they should be kept in mind.

With but one exception, Federal forest entomologists conduct their work out of Forest Service regional experiment stations and the Alaska Research Center. The exception referred to is the work on airplane spraying and the use of radioisotopes,

which is conducted at the Beltsville, Maryland, Forest Insect Laboratory. Results of the work at this Laboratory have nation-wide application.

During past years, because of differences in degree of demand for protection from forest insects, the intensity of research in various parts of the country has varied widely. Considerable attention has been paid to problems in the Northeast, and in the Far West and Northern Rockies. In contrast, almost nothing has been learned of the habits, behavior, and control of damaging species in the Southwest. Plans are currently underway to remedy this situation by strengthening the work in the regions which have received but little attention in the past. Timber owners in all regions are now clamoring for assistance in the control of destructive forest pests.

### DIRECT CONTROL

Generally speaking, the status of research on the direct control of forest insects in the United States is good. Materials, methods, and techniques have been developed which can be applied to suppress outbreaks of most of our destructive species. Weak spots occur, of course, and some of them are of great concern to us; but perhaps that is to be expected. We have reason to hope that added research will enable us to strengthen them.

The control of outbreaks of certain defoliating insects in widespread forest areas was, until just a few years ago, impracticable if not impossible. Today it is in large part commonplace. The availability of the highly potent insecticide, DDT, which can be applied in a concentrated form by means of aircraft, has made this possible.

The control of many species of destructive bark beetles has been simplified and made more economical through the formulation of insecticides containing benzene hexachloride. The same is true of insecticides containing ethylene dibromide. Development of techniques of application have made it possible in many instances to treat trees while still standing. The discovery that some of these materials are effective as water emulsions against certain species has greatly reduced control costs. Where emulsions can be used, it is no longer necessary to transport huge quantities of oil into the forest, sometimes for long distances into remote, roadless areas. Water, as a substitute for oil, is usually present in sufficient quantity near the site of the control operation.

The direct control of outbreaks is becoming more practicable each year, also, as a result of the expansion of survey activities throughout the Nation. It is much less likely now that an outbreak can occur and expand into unmanageable size before it is detected. This is permitting the application of direct measures to an increasing proportion of outbreaks while they are still in their formative stages. The success of surveys hinges strongly on the use of accurate and economical methods. Considerable information is already available on the economical and effective use of aircraft in conducting surveys. Significant improvements in the conduct of ground surveys, many of which still are necessary, have also been made recently. These developments, plus the wider use of more effective chemicals, have greatly improved the status of direct control in the United States.

The Forest Service will continue its research in the direct control of insects. Major attention will be given to the development of methods not now available for the control of certain important species; to the screening of new insecticides in the continuing search for more effective, economical, and safer ones; and in the improvement of application techniques. We do not foresee the time when it will be possible to dispense with direct control methods altogether. We are certain that the Law of Diminishing Returns is not operating against us in much of our effort to improve upon existing methods. It will be a long time before we have any good idea as to the best materials and methods to use against many of the vast assortment of insects with which we are forced to contend in the forests of our country.

### BIOLOGICAL CONTROL

The status of research on the biological control of forest insects in the United States is not so good as that of direct control, but the trend is encouraging. Forest entomologists in the States have long been conscious of the role of parasites, predators,

and diseases in controlling certain infestations of insects. Taken altogether, a considerable amount of research has been conducted on these control factors. For example, for many years an all-out effort was made to control the gypsy moth in the Northeast by the introduction and establishment in infested areas of its parasitic and predacious enemies from abroad. The general impression now is that this work was successful; so much so, in fact, that the gypsy moth now appears to react much in the manner of a native insect in a large portion of the older areas of infestation in New England.

In recent years research on biological control has occupied a minor position in the program of the Forest Service. Nevertheless, significant progress has been made in this difficult field. For example, mention might be made of the work which has been underway for several years on the spruce budworm in the Northeast. Results of this work have been especially encouraging since they have provided a means whereby it is possible to predict, on the basis of parasite presence and abundance, the trend of the budworm population. This has proved very helpful in appraising the significance of infestations, and in determining possible needs for direct control. Similar studies have recently been initiated or proposed in budworm infested stands in the Lake States, the Rocky Mountains, and Pacific Northwest. Many other biological control studies on a smaller scale are underway on several other pest species in various parts of the country. In most of these, however, efforts currently are being confined largely to the determination of biological factors. It is only in the occasional instance that efforts are being made to evaluate their effectiveness.

There is considerable current interest in the States in the possibilities of forest insect control through the use of virus diseases. Since the very beginning of forest insect work in the country, entomologists have observed the catastrophic ending of certain insect outbreaks by disease. Several decades ago the causative organism of at least one of these diseases, the so-called wilt disease of the gypsy moth, was determined to be of virus origin. It was not until recently, however, that entomologists learned how to collect, preserve, and propagate disease-causing virus organisms. Credit for this development belongs to our friendly neighbors to the North, the Canadians. They were, however, kind enough to let us in on the secret. Furthermore, they came down and gave us a lift in getting started in the work. I refer, of course, to studies of the virus of the European pine sawfly. We were quick to learn. Now we unhesitatingly apply solutions of the virus by means of airplanes to sawfly-infested plantations, with consistently good results. This work has stimulated interest among researchers throughout the country to be on the lookout for evidence of disease in infestations of many kinds of insects. When these are encountered, specimens of diseased insects are collected and transmitted to disease specialists for identification. Recently, the Forest Service cooperated with disease specialists in the Entomology Research Branch, Agricultural Research Service, Department of Agriculture, in studies of a virus affecting the Virginia pine sawfly (*Neodiprion pratti pratti* (Dyer)). It has been shown experimentally that this virus also can be used in the form of a spray to reduce populations of the sawfly. I could cite several other instances of our work with viruses, but time and space do not permit. Suffice it to say that we will spend a lot more time in the next few years exploring the possibilities of this method of forest insect control.

The trend in biological control research, therefore, is definitely encouraging. As time and facilities permit, more and more emphasis will be placed on this phase of our work.

### SILVICULTURAL CONTROL

Under this heading we will discuss the status and trends of work on the control of forest insects through modifications in management practices, and by other procedures whereby the environment may be rendered less suitable for the development of destructive insect infestations. There are not a great many instances where prescribed management methods have been worked out for the alleviation or prevention of insect-caused losses. There are, however, numerous observations on record of the relation of outbreaks to stand or site conditions.

Entomologists have known for a long time that certain species of insects, especially the bark beetles, tend to attack or damage trees of low vigor. This suggested

a means of preventive control; namely, by the systematic classification of trees into vigor classes and the removal of those most susceptible to attack. Now, after several years of study, it has been abundantly shown that this method of control of the western pine beetle is successful in large portions of the ponderosa pine region of the West. The remarkable thing about it is that the work can be done at a profit to the timber owner. The salvage and sale of the susceptible trees in a stand renders the residual stand relatively safe from destructive attack by the beetle for several years. Comparable results are following similar work with the Jeffrey pine beetle. Results of this research have been so outstandingly successful that studies are being expanded to include other species of bark beetles infesting other pines in different parts of the country.

It was determined several years ago that outbreaks of the gypsy moth tended to develop in hardwood stands containing high proportions of trees of certain tree species. It was also shown that stands of these trees tended to occur most frequently on dry, exposed sites. This suggested a means of reducing damage by this insect through transformation of these stands to those containing a preponderance of less favored trees. It also assisted in the delineation of areas outside the area of infestation that might be expected to harbor destructive populations in case of further spread of the insect into uninfested regions.

The spruce budworm is most destructive in northeastern United States in mature stands of balsam fir. Management practices designed to harvest this timber before it becomes most susceptible reduces damage by this insect. The jack-pine budworm in the Lake States region is most damaging in stands containing an abundance of staminate flower-bearing trees, or in stands containing over-topping wolf trees. Damage resulting from defoliation can be reduced by management practices designed to remove or greatly reduce the abundance of these trees in stands. The locust borer attacks trees in all degrees of vigor but is only destructive in those of low vigor.

Outbreaks of the black turpentine beetle are encouraged or abetted by naval stores operations; outbreaks of *Ips* spp. follow in the wake of fire, storms, and drought. Explosive populations of the Engelmann spruce beetle and Douglas-fir beetle in the West have followed in the wake of extensive blowdowns. Knowledge of these facts suggests that management practices are possible that will lessen the incidence of destructive outbreaks.

In the years ahead, forest entomologists, working hand in hand with specialists in forest management, will intensify their efforts to determine management practices best suited for the development of forest stands that are least susceptible to insect outbreaks. In many instances we know that success will not come easily. Complications will arise in those stands susceptible to attack by more than one destructive insect species, inasmuch as conditions required for the control of one may not always coincide with those required of the other. Furthermore, we know that before complete protection can be guaranteed we must possess much more knowledge than we now do on other factors which also affect insect populations. Entomologists are aware that the effects of these other factors, some of which remain obscure, are sometimes overriding, and that stand conditions alone do not always determine the trends of infestations.

### MISCELLANEOUS RESEARCH

The foregoing discussion does not cover all of the research on forest insects in the United States. Other lines of work, some of which I might have squeezed in under one or more of the above headings, are also being followed. Here, I have in mind such studies as those on insect life histories; on the use of radioisotopes in tracing the flight pattern of insects; insect control through the use of resistant strains, or hybrids, of trees in planting programs; the role of insects in the transmission of tree diseases; the possibilities of insect control through the use of systemic insecticides; improvements in survey techniques; and in the control of insects affecting wood products.

In many sections of the country, chiefly in the South and Southwest, much less is known of the biologies of forest insects than in other sections. Efforts are being made to remedy this situation as fast as possible. In many important instances the



development of satisfactory provisional methods of control are being hampered by a lack of knowledge of insect life histories. We will expand our work of this nature in the more neglected sections of the country during the next few years.

The Forest Service has not made a great deal of progress so far in its studies of insect control through the use of resistant strains or hybrids of trees. We think this is largely because only a small amount of research has been devoted to the subject during past years. We have learned enough already, however, to indicate that considerable relief might be obtained from the ravages of many pests by the more extensive use of resistant or less susceptible planting stock in reforestation programs. So far, with the help of Forest Service geneticists, we have found that the pine reproduction weevil, a serious pest of Jeffrey and ponderosa pine seedlings in California brushfield plantations, can be controlled by the planting of seedlings of a cross between highly susceptible Jeffrey pine and non-susceptible Coulter pine. This is proving economically feasible because the hybrid not only inherits resistance factors from Coulter pine but, also, desirable growth characteristics from Jeffrey pine. In order to fully explore the possibilities of this kind of insect control, the Forest Service is expanding its research on the problem as rapidly as possible.

We have done a little work with radioactive tracers in studying the flight habits of insects. Most of it has been with the Engelmann spruce beetle in Colorado. We have by no means made an exhaustive study of the materials in tracing insect flight patterns. So far, considerable time has been devoted to developing techniques for study. We believe we have made progress along these lines. In our work on the Engelmann spruce beetle, we were able to locate tagged insects under the bark of logs at distances of at least 3 miles from the release point. More recently we have attempted to trace the movements of the southern pine beetle, of white pine weevils in white pine plantations, and of white grubs in the soil. Final results are not yet available for analyses. We will continue our studies with radioisotopes for the time being — at least until we have a better idea of their value in forest insect research.

Forest entomologists in the States have been very successful in studies of insect vectors of epidemic tree diseases. Several years ago they determined the role of elm bark beetles in the spread of the fungus which causes Dutch elm disease, a deadly disease of American elm trees. They found that while the chief vector in the United States was the smaller European elm bark beetle, *Scolytus multistriatus* (Marsh.), the fungus was also transmitted by the native elm bark beetle, *Hylurgopinus rufipes* (Eichh.). Later they learned how to prevent or greatly reduce the incidence of disease through the control of its insect vectors. In more recent years, entomologists also discovered the insect vector of elm phloem necrosis, a virus disease of American elm. Again, through intensive research, direct control methods for use against the leafhopper vector were developed. At present, studies are underway to determine the role of insects in the transmission of oak wilt, a disease which threatens the existence of the vast oak stands of eastern United States. Entomologists in the employment of several of the affected states are also working on this problem. So far it is proving a most difficult one to solve. It has already been determined, of course, that many different kinds of insects are capable of transmission. There is good reason to believe that the primary vector species will soon be determined — assuming, of course, that any one such species actually exists in nature.

The Forest Service recently initiated research into the possibilities of controlling insects in living trees with systemic chemicals. Most of the work to date has been concerned with the development of techniques for testing candidate chemicals. What was needed first was a simple and effective method for determining the presence of translocated chemicals in various plant pests after treatment. Our entomologists have developed an effective method which involves the use of a small crustacean, *Daphnia* sp., as a test animal. This organism is highly susceptible to toxic substances. As a result, minute quantities of the substances can be detected in plants — much smaller quantities, in fact, than could be detected by any other equally simple device that we know of at this time. I will not attempt to describe the technique here. Suffice it to say that it is effective and should prove helpful in future studies of insect control through the



use of systemics. This work will be continued and expanded where possible during the next few years. We are hopeful that we may one day come up with a chemical which can be applied to entire stands, preferably from aircraft, to render them resistant to injury by certain insect species. While this may, at first glance, appear to border on the fantastic, we should not be forgetful of the fact that all species of trees already are either unattractive or immune to damage by the vast majority of insect species. Nature, it seems, has long since been doing what we are only now attempting to do; namely, incorporating into trees substances either toxic or repellent to most insect species.

One of the most productive lines of research in forest insects in recent years has been that connected with the improvement of survey techniques. Surveys of a sort have been conducted on many species for years. Many of the techniques employed were adequate for determining the status of infestations and the need for direct control. In few instances, however, was it known whether they were the most accurate, the most rapid, or the most economical ones that could be employed. Because of the ever-mounting pressure during the past few years for increased accuracy and speed in the detection and evaluation of insect infestations, it became necessary for us to expand our research in the improvement of survey methods. Great strides have since been made in the development of aerial methods. This not only has made it possible to provide greater coverage of forested areas but has also reduced costs of surveying some insects almost to the point of absurdity. There are other insects, however, that must be surveyed from the ground. By comparison, these surveys are infinitely slower and much more costly than those made from the air. Much progress has been made recently, however, in speeding them up, improving their accuracy, and reducing their costs. For example, sequential sampling methods have been worked out for a few species, thereby greatly simplifying the job and reducing the cost of surveying for them. There is much more that remains to be done before the most accurate, rapid, and economical survey techniques can be worked out for a host of insects in our forests. There will be a lot of activity along these lines in the next few years.

In some respects, the status of research on insects affecting wood products is good — especially in the eastern part of the country. Considerable knowledge is available on the insects that damage wood in the latter area. Some of these insects, as most of you already know, begin attacking timber as soon as it is cut in the woods, and others continue to attack long after the wood has been processed and placed in structures. Materials and methods for use in controlling or preventing damaging infestations have been developed for use against most major species. Notable advances have been made with several of the new insecticides which have become available since World War II. Some of these are being used in tests against such notorious pests as the eastern subterranean termite and *Lyctus* powder-post beetles and are giving highly promising results. Used against termites as soil poisons, some are giving long-lasting protection — just how long remains to be determined, since many are still effective even after exposure periods of 5 to 10 or more years. Work will be continued to determine the most effective and economical methods to use in controlling or preventing infestations of these insects. As soon as we are able to do so, we will expand our research on these insects to include western parts of the country.

### CONCLUSIONS

In the time allotted to me on this program, I have been able to touch only upon the highlights of the status and trends of forest insect research in the United States. I hope, however, that I have succeeded in indicating roughly where we stand and where, and how we expect to go from here. In bringing this discussion to a close, I should like to make it clear that our research in the next few years will be more strongly pointed towards the goal of preventive entomology. We think we have attained a respectable position in many parts of the country with regard to the possibilities of direct control. To the extent that this is true, our greatest future needs, as we now see them, lie in learning as much as we can, as quickly as we can, about the possibilities of preventing destructive insect outbreaks. We have no illusions about the magnitude

of the problems facing us in this difficult field of research. They are going to be hard to solve and, even if we succeed in solving them, we realize that results will often be slow in coming. It may also be many years before we can devote our major efforts to this type of research. There is still a lot of work to be done on many destructive insects before we can relax our efforts too much in the development of provisional control methods. Nevertheless, the need for this type of work is narrowing. We already are beginning the slow process of shifting the direction of our program towards the goal of preventive entomology. In the coming years I think we may expect an increase in the momentum of our rate of change in this direction.

# Some Insects of Forest Trees in New Guinea

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## ABSTRACT

*Eucalyptus deglupta* (Blume) ("kamerere") is distributed in the Southern Philippines (Mindanao), Celebes, coastal New Britain, and on the mineral soils of active volcanoes up to 6000 feet, the lower flats of the Waria Valley in northeastern New Guinea, and in isolated places in the Wahgi and Jimmi Valleys of the central highlands of New Guinea. There is some evidence that *Eucalyptus deglupta* may be a relic species in the New Guinea highlands having persisted over a considerable period during the gradual uplift of the central plateau of New Guinea.

The Australian saturniid *Capaxa janetta* White and the leafcutting bee *Megachile lachesis* (Sm.) were observed damaging leaves of *Eucalyptus deglupta* in the highlands of New Guinea in 1954-1955. A coreid (Leptoglossus) and pentatomid (Austromalaya) appeared in plague form on young kamerere trees, planted by the Department of Forests near Port Moresby, causing large-scale wilting and die-back of leaves. A tachinid was found parasitizing *Capaxa janetta* and a reduviid preying upon *Leptoglossus* and *Austromalaya*.

The defoliation of *Tectona grandis* by the noctuid *Hyblaea puera* was repeatedly observed in New Britain. The ichneumonid *Ectromorpha insidiator* (Smith) was found as a parasite.

The curculionid *Vanapa oberthuri* causes some damage to plantations of hoop pine (*Araucaria cunninghamii*) and has been found in natural hoop pine forests in Papua and New Guinea. Where heavy infestation occurs, trees up to 30 feet high and 10 inches in diameter have been killed. This insect could become a serious pest of hoop pine plantations.

*Eucalyptus deglupta*, family Myrtaceae, is indigenous to parts of New Britain, mainly the coastal areas of the north and south coast of the eastern end of the Island where it forms almost pure stands in river valleys. It is also known as a colonizer of the bare mineral soils of some of the active volcanoes up to an altitude of 6,000 feet. It also occurs in the lower Waria Valley on the northeast coast of New Guinea and has been found in recent years in the Wahgi and Jimmi Valleys of the Central Highlands. As in New Britain, it is associated with rivers although the areas of each stand are much smaller. Seed germination takes place only on a mineral soil exposed to a high light intensity and, therefore, sandbanks left after river flooding can become colonized. *Eucalyptus deglupta* is also known to occur in the Celebes and southern provinces of the Philippine Islands. It is of interest to consider how *Eucalyptus deglupta* may occur in the Central Highlands of New Guinea. This species has apparently evolved under tropical conditions and is not closely related to any Australian representatives of this genus. We may therefore postulate that at least a precursor of modern *Eucalyptus deglupta* was cut off by the disruption of land barriers between New Guinea — Celebes — Philippine Island chain, and Australia relatively early in the development of the genus *Eucalyptus*. There is no reason to suppose that the present day occurrence of *Eucalyptus deglupta* in the Central Highlands is in any way a recent establishment.

If the trees were actively invading favourable sites many places in New Guinea have large sandbanks available for colonization and these would undoubtedly be carrying stands of this tree. It may well be, although observational proof is as yet lacking, that this species together with a number of other plants now found in the Central Highlands

are relics of the vegetation before the late tertiary uplift of the main mountain ranges of New Guinea took place. The other occurrence on the New Guinea mainland in the lower Waria Valley may readily be explained by wind-blown seed from New Britain fortuitously falling on a suitable seed bed within quite recent times.

The larvae of *Capaxa janetta* White, a medium sized saturniid, have been found damaging the foliage of *Eucalyptus deglupta* in the Eastern Highlands. The light apple-green larvae have two rows of tubercles on the dorsal surface of the meso- and meta-thoracic segments and of the abdomen, on each side of the median line. The fleshy tubercles end in small orange knobs armed with a long black central spine and five short lateral spines. The four thoracic tubercles are longer than the abdominal tubercles. There is also a long dorsal tubercle of similar appearance in the middle of the second last abdominal segment. A conspicuous lemon-yellow lateral line decorates the abdomen below the tubercles. The reddish-brown legs are relatively short, the four propodia fairly large. The fully grown larvae are up to 90 mm. long and 15 mm. wide. The freshly woven cocoons are greenish golden-yellow which later change to light brown.

The adults show a large individual variation of the coloration of the wings from light yellow to dark reddish-brown, similar to the specimens found in Australia. *C. janetta* does not seem to form a geographical variety (subspecies) in New Guinea. To the best of our knowledge this species was not recorded so far from the Territory of New Guinea. Apart from its occurrence in the Eastern Highlands, adult specimens were collected by N. Blood at Nondugl (Western Highlands) and by W. Brandt at Subitana, Central District of Papua, about 1800 feet above sea level.

Most of the trees in the town area of Goroka (5200 feet) are almost continually attacked by the larvae of *C. janetta*. It is not a seasonal insect in the Highlands of New Guinea. Larvae of various ages, cocoons, and adult moths can be found throughout the year. As many as 45 fully grown larvae and 38 cocoons could be found on 1- or 1½-year-old trees.

Defoliation is not very severe and does not cause a serious setback in growth, unless the trees are simultaneously attacked by the leafcutting bee *Megachile lachesis* Sm. (var.?). This megachilid is widely distributed over the Mainland of New Guinea. The stripping of the leaves by the bees changes the whole appearance of the trees and by the cutting of more or less symmetrical circles and ovals, the shape of the leaves resembles that of *Quercus* spp. The joint attack of *M. lachesis* and *C. janetta* causes quite a serious setback to the growth of young trees. Some of the entirely defoliated branches become dry and die.

Only one parasite, the tachinid *Cuphocera varia sumatrensis* Tns. was reared from the cocoons of *C. janetta* but the percentage of parasitism was very low.

Three hemipterous pests of *Eucalyptus deglupta* were observed attacking young trees in the plantation of the Department of forests at the Brown River, near Port Moresby (Central District of Papua). These were the coreid *Leptoglossus australis* F. (a well known pest of *Passiflora* in New Guinea), a large grey pentatomid of the genus *Austromalaya*, and the flattid *Paratella errudita* Melich. The appearance of *Leptoglossus australis* F. as a pest on *Eucalyptus deglupta* is rather unusual, although this coreid has many subsidiary hostplants besides *Passiflora*. A species of *Austromalaya* was earlier observed as a pest of *Theobroma cacao* (Dumbleton 1954, Dun 1954). The three hemipterons appeared in the *Eucalyptus deglupta* plantation simultaneously in very large numbers. None of these insects could have caused extensive damage alone, but the joint attack of the three sap-sucking insects on the leaves and the branches caused serious defoliation and a certain degree of setback in growth. When the senior author visited the area at the end of September 1955, many branches of the young trees were bare and most of the remaining leaves were wilting and drooping, showing bright yellow, reddish-brown, and dark brown colours. The plantation had an appearance of a temperate climate forest in late autumn. However, the serious outbreaks of the three hemipterous pests had ceased shortly after the senior author's visit, apparently halted by the reduviid *Graptoclopius pallescens* which was present in large numbers at the time of the visit when it was observed preying upon nymphs of *Paratella errudita*, *Lepto-*

*glossus australis*, and *Austromalaya* sp. Another reduviid (*Helonotus* sp.) was found preying upon the nymphs of *Leptoglossus australis* F.

It is very likely that there was also an upset in the balance of hosts and egg-parasites, which could have caused the appearance of the three hemipterons in unusually large numbers during the extreme dry season of 1955. The young trees rapidly recovered after the disappearance of the pests. Vigorous green leaves covered the branches at the beginning of the wet season when observed by officers of the Department of Forests, Port Moresby.

An alticid, *Arsipoda* sp., was found causing serious shot hole damage to the tender leaves of *Eucalyptus deglupta* seedlings at the Brown River in December 1955. Various alticids, damaging young coffee trees and other cultivated plants in New Guinea were easily controlled with a spray of 0.2% DDT and 0.15% Dieldrin spray. This appeared to be unnecessary in the case of *Eucalyptus deglupta* seedlings, because the outbreak did not last long. There was no severe setback in the growth and as the seedlings grew and the surface of the leaves lost its tenderness, the polyphagous alticids left the seedlings and found subsidiary host-plants amongst the weeds of the surrounding area.

The widely distributed agrotid *Hyblaea puera* Cram. was repeatedly defoliating the seedlings of *Tectona grandis* in the nursery of the Department of Forests at Keravat Sawmill (Gazelle Peninsula of New Britain). The senior author also observed the defoliation of 4- to 5-year-old trees in the Teak Forest, planted by the Department of Forests at Keravat, but the older trees were not affected so severely as the young, tender seedlings. When the senior author visited the nursery in December 1954, larvae, pupae, and adults of *H. puera* could be found on practically every seedling of the nursery. Dusting with 10% BHC powder had to be repeated several times at short intervals during the campaign against this serious pest of *T. grandis*.

In a recent communication on *H. puera* Mr. A. Richardson, Senior Forest Officer (Rabaul) stated that a certain degree of seasonalism can be observed in New Britain. The adult populations reach their peak twice per year—in May or June and in November or December.

*H. puera* has a very wide geographical distribution. This insect has been recorded from India to Formosa, and from South China to Australia. It was introduced to Jamaica. Thompson (1946) records 23 parasites of *H. puera* from this vast area—8 ichneumonids, 8 tachinids, 3 braconids, 3 chalcids and 1 elasmid, most of them larval parasites. Only one parasite, the polyphagous ichneumonid *Echtmorpha insidiator* (Smith) was reared from pupae of *H. puera* at Keravat but the degree of parasitism was very low. This shows that there was an upset in the balance of parasites and host, most likely as a result of the extreme dry season of 1955. *Echtmorpha insidiator* as a parasite of *H. puera* represents a new record.

Larvae and several parasitized pupae of *H. puera* were found by the senior author in 1955 in the teak nursery of the Department of Forests at Port Moresby, but no serious damage could be observed, apparently as a result of the high percentage of parasitism. The recorded food plant of *H. puera* in Australia is *Vitex trifolia*, family Verbenaceae, which grows as a shrub in poor soils and as tree on better soils in Malaya. Its distribution ranges from the Himalayas to Ceylon, the Philippines, Japan, Malacca, New Guinea, and northern Australia.

*Vanapa oberthuri* Poir., a large curculionid, appeared to cause considerable damage to Hoop Pine (*Araucaria cunninghamii*) in the Eastern Highlands of New Guinea. The infestation of hoop pines by this weevil was first noticed at Highlands Agricultural Experiment Station, Aiyura (Kainantu Subdistrict of the Eastern Highlands District), about 5500 feet above sea level. Specimens of the adult beetle were forwarded to Sir Guy Marshall for identification. This weevil was very little known in collections prior to its discovery at Aiyura. The type and paratypes were collected by Oberthur in the upper valley of the Vanapa River and the species was also found by Pratt in the area of the Angi Lakes. The species is apparently unknown outside of New Guinea.

The attack by *V. oberthuri* was first investigated by the junior author in November 1950. Further investigations and observations on the life history were made in July 1951



by officers of the Department of Agriculture. They found that the female appears to puncture the bark and places the rather long (up to  $\frac{1}{4}$  inch) cream-coloured egg in the crack. Eggs are deposited singly in clean smooth patches of bark. The eggs were not laid in existing resin flows nor does it seem likely that the puncture made by the females causes any resin flow.

The very youngest larvae observed were associated with copious resin flows within which the frass is discernible. Careful examination revealed that very little attack on the bark had occurred at this stage. It appeared that the larva had travelled to a point where resin was flowing, or where there was easy access to the sapwood.

Burrowing into the bark and the sapwood starts when the larva is about  $\frac{1}{2}$  inch long. A hole up to  $\frac{1}{2}$  inch in diameter is formed more or less radially into the trunk for a depth of  $1\frac{1}{2}$ -2 inches. By then the larva has grown considerably and exceeds 1 inch in length and  $\frac{3}{8}$  inch in diameter. The hole turns towards the vertical and the pupal cavity is made parallel with the long axis of the tree. This chamber is blocked by a curious conical plug, formed at its base of finely comminuted wood, but the upper distal part is composed of shreds of wood fibre perhaps 1 inch long by  $\frac{1}{20}$  inch wide. It has not been ascertained whether emergence takes place through the entry tube after removal of the plug or by a new hole. The latter seems very unlikely.

Individual trees become heavily attacked and die. In heavily infested areas trees up to 30 feet high and 10 inches in diameter have been killed. A length of tree bole, approximately 5 feet long and 8 inches in diameter, which had been cut because borer attack was visible and the tree was dying, yielded seven healthy larvae and six pupae.

The following control measures were applied at Aiyura. All badly infested trees were felled and burnt; mildly infested ones were not cut out but adults and larvae found inhabiting the tree were destroyed with a short length of sharpened wire. Inspections of the older stands were carried out at regular intervals. Every tree was examined but little time was spent on those showing no evidence of the female weevil's presence.

The adult beetle appears to move very little on its egg laying excursions which is proved by the fact that there are definite foci of infestation in the hoop pine plantation. Quite frequently one finds a group of five or six trees which have all suffered to some degree the depredations of the insect.

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# Some Recent Research on Forest Insects in New York State

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## ABSTRACT

*This paper presents some background information on the current forest insect situation in New York State, and gives a brief orientation in the problems currently under study by the State Entomologist's office. Among the insects discussed are the white pine weevil, *Pissodes strobi* (Peck); the European pine shoot moth, *Rhyacionia buoliana* (Schiff.); other plantation insects including *Ips pini* (Say); the forest tent caterpillar, *Malacosoma disstria* Hbn.; insects which attack windthrown or storm-damaged timber; and insects which attack saw logs, both in decks in the woods and in storage yards, principally *Scolytidae* and *Cerambycidae*.*

Ever since its establishment in May, 1854, the office of the State Entomologist has been concerned with forest insects. After the formation of the State Agricultural experiment Stations at Geneva and Cornell University, with these stations concentrating on agricultural pests, and the State College of Forestry at Syracuse, where the entomological work has been largely teaching, the State Entomologist's office in Albany continued to be largely concerned with forest insect problems. Since the principal state agency working on forest problems in general is the Conservation Department, also with headquarters in Albany, it is natural that a mutual assistance relationship has arisen between the two groups.

The Conservation Department administers the State Forest Preserve and other forest lands belonging to the state, and the State Entomologist's office is frequently consulted when forest insect problems arise, especially in the Forest Preserve and in the state reforestation plantings. When a problem is such that research is needed to supply additional information, this research may be undertaken as a joint project of the State Entomologist's office and the Bureau of Forest Pest Control of the State Conservation Department. The U.S. Forest Service is usually consulted, and is frequently another collaborator in the joint project. Sometimes also, a project may be initiated or suggested by the Forest Service, especially when it is of such a nature that data from New York State are needed to fill out the picture in a problem in which several states have an interest.

The present paper gives an account of several forest insect research projects in which the State Entomologist's office has been a principal participant during the past five years, and in which it is believed that significant information, leading to a better understanding of the problem, or toward a better control of a pest, has been obtained.

A synoptic style of presentation based on a brief discussion of the work done on each pest has been adopted as best suited to the purpose, since details on some of the problems may be more fully set forth elsewhere by collaborators, in more extended special reports.<sup>1</sup>

The accompanying map of New York (Fig. 1) shows the locations where certain pests have occurred in sufficient numbers to warrant the establishment of (1) research projects; (2) the setting up of study plots; or (3) the application of a large scale

<sup>1</sup> Connola, D. P., D. L. Collins, J. H. Risley and W. E. Smith. 1956. Insect damage and its prevention in windthrown saw timber. *New York State Museum and Science Service Bul. No.* 352.

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control measure, either on a practical or an experimental basis. The map does not necessarily give any idea of the distribution or relative abundance of the species shown. Of the species indicated, or problems implied, the following have been selected for discussion.

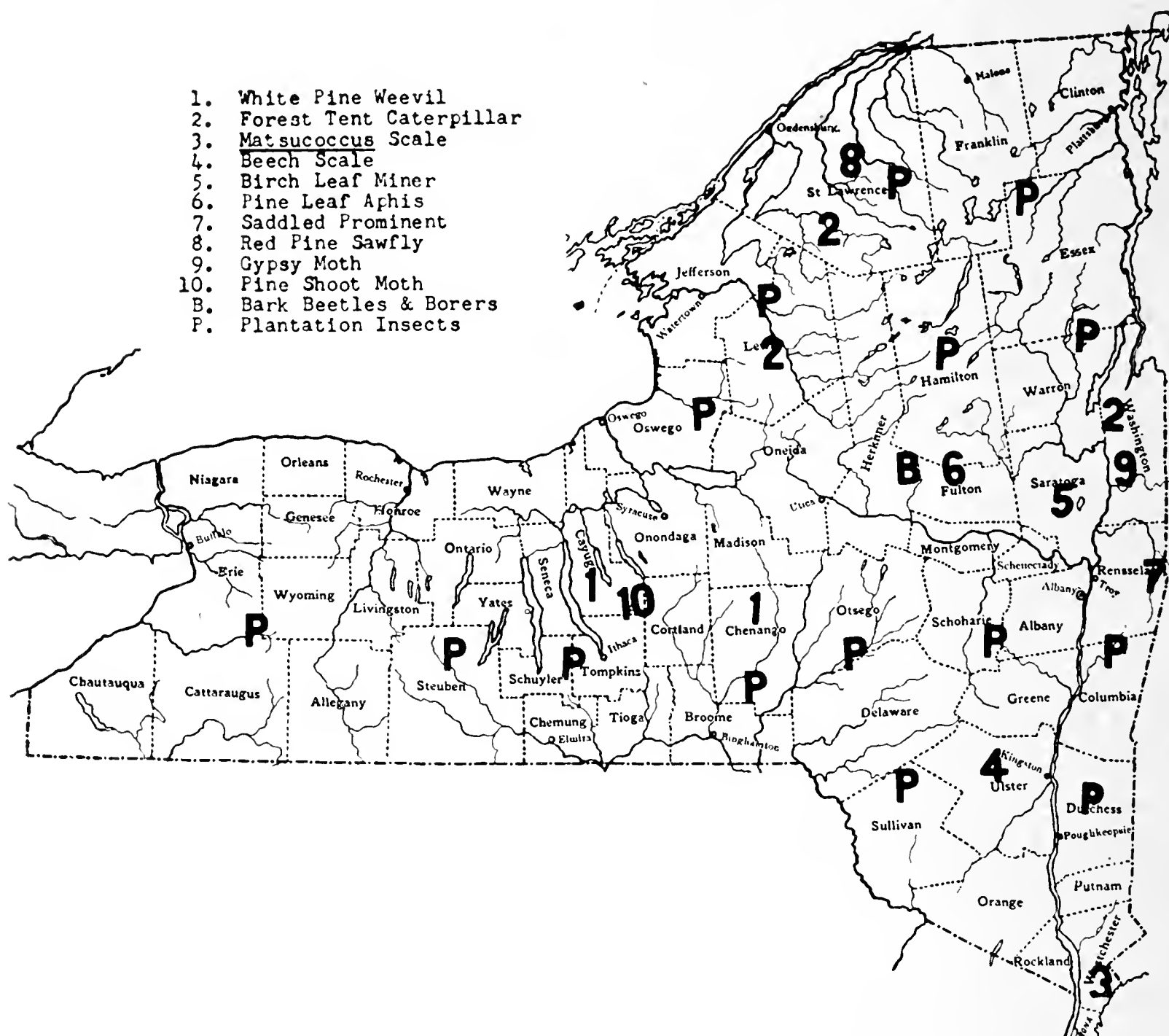


Fig. 1. Map of New York State showing location of forest insect experimental areas and study plots.

WHITE PINE WEEVIL, *Pissodes strobi* (Peck). The white pine weevil (No. 1 in Fig. 1) is the number one pest of white pine *Pinus strobus* (L.) in New York. Its damage to terminals causes trees not only to lose two to three years' growth but also to fork or grow crooked, thus reducing their value as timber trees. Studies of its control by spraying have been under way for five years in cooperation with the Conservation Department and the U.S. Forest Service. Airplane spray tests with 2 pounds of DDT in 2 gallons of kerosene per acre in white pine plantations showed that this quantity of DDT was not sufficient to produce control when applied by fixed-wing planes. However, when the dosage was doubled, by applying two sprays, one following the other, each at the rate of 2 pounds per acre, giving a total dosage of 4 pounds per acre, weeviling was reduced from 50% to 2% in one plot of 10 acres, and from 50% to 2% in another plot of 10 acres. In the latter there was a two-week interval between sprays.

In the first plot it took three years for the weeviling to reach the same level it held before spraying. In the second plot, after three years, weeviling was still 10 percent lower than it had been prior to spraying. These results prompted further tests, begun in 1956, to improve application techniques. The delivery rate of the spray was increased so that 4 gallons per acre could be applied in one operation. This was done by using larger nozzle openings. However, this resulted in a larger average droplet size and the distribution of spray was not so good as it was when the same dosage was applied by two consecutive passages at half the dosage. Although the weeviling was reduced to

3.6 percent from 33 percent, and represented an 89 percent reduction from the check, it was felt that the residual weevil population would permit a faster buildup than the earlier 2-spray technique, by which weeviling had been reduced to 2 percent.

It is suggested that a better spray pattern can be achieved by increasing the number of nozzles and reducing the size of the orifices. This possibility is now being investigated.

A study of environmental factors which may influence the amount of weeviling which occurs in a white pine plantation was begun in 1954. In this study, one-tenth acre sample plots are being established in each forest district of the state (letter P in Fig. 1). Although these studies are not complete, it is indicated from 95 sample plots that soil type and drainage may be important factors in the white pine weevil problem. Trees planted on the heavier soils in the south central and eastern portions of the state appear to be more heavily attacked than trees planted on lighter soils.

FOREST TENT CATERPILLAR, *Malacosoma disstria* Hbn. A heavy outbreak of the forest tent caterpillar reached a peak in New York State in 1954. Beginning in 1951, with considerable foliage damaged on 110,000 acres of forest land in northern New York, in 1954 the severely infested area included some 15,321,407 acres, as determined by airplane surveys. In 1955, the intensity of the outbreak diminished and the population began to decline until there were comparatively few areas of severe defoliation in 1956.

The outbreak afforded opportunity to make several interesting studies. Preferred host trees included primarily aspen (*Populus* sp.) and sugar maple (*Acer saccharum* Marsh). It was found that in special-use areas such as state campsites and around lakes where heavy summer resident populations demanded it, virtually complete control could be obtained by an aerial spray of 1 gallon of kerosene containing one-half pound of DDT (i.e., an approximately 6% solution of DDT), per acre. Maple sugar grove owners, through cooperative agreements between owners, the counties and the state, obtained similar protection of their sugar maples in 1953 and 1954. The cost of spraying was less than \$2.00 per acre.

Studies to determine (1) the extent to which repeated defoliation actually damaged sugar maple trees and (2) the effect on the quantity and quality of the sap were undertaken in the Lake George area, and are being continued for a five-year period. Thus far three years of data have been collected. Although defoliation on some of the plots in 1956 was not so heavy as in previous years, mature trees which had suffered heavy defoliation earlier appeared to show more dead wood in their crowns than trees which were not defoliated so heavily. Data on hand also show that sugar content of the sap was lowered when defoliation reached heavy proportions. Trees that are severely damaged, according to present indications, may never fully recover their former productivity.

Annual egg mass surveys were made each fall and winter during the forest tent caterpillar outbreak to determine its general course, and to afford a basis for predicting heavy defoliation and where control might be needed. These surveys afforded an opportunity to test the sequential sampling technique.

By this method, egg mass sampling is carried on until the counts classify the infestation. In our surveys, ten 30-inch branches examined from each tree or group of small trees constituted a sample from which egg mass counts were made. The counts were referred to a table which classified them. The table was derived from data taken in previous years. The classification either predicted noticeable defoliation for the next season or no noticeable defoliation, or indicated that sampling should be continued. If the latter was the case, ten-branch sample units were taken from other trees nearby until the cumulative count of egg masses classified the infestation. In most cases only three or four sample units were necessary from one location to classify the infestation. Often only two samples were necessary. Most of the sampling was done on poplar and sugar maple.

Near Lake Ozonia, in northern New York, where damage had declined, tests with the sequential sampling technique indicated that the method is valid only when the insect outbreak is new, or at its peak. This would be expected, since statistics were based on data collected early in the outbreak. The sequential sampling technique proved to be both more rapid and more accurate than the sampling methods formerly used.



A comparison with the older method of collecting a fixed number of samples (25) from each location showed that the sequential method saved 87 percent in man-hours required. This saving in time and labor appeared to be its greatest asset.

A method of sequential sampling is now being devised for the red pine sawfly, *Neodiprion nanulus* Schedl. Correlation data between egg deposit and defoliation are being collected on 25 sample plots in red pine (*Pinus resinosa* Ait.) stands in St. Lawrence County (No. 8 in Fig. 1).

FOREST PLANTATION INSECTS IN RELATION TO SILVICULTURAL PRACTICES. This is a field in which there appears to be little information. In New York State at least, and also in many other areas, this lack of information is now being keenly felt, since so many forest plantations have reached the stage where a decision must be made on what thinning and other silvicultural practices must be followed. Accordingly, a joint study by the Conservation Department and the State Entomologist's office of the State Science Service has been undertaken. Briefly, the study is concerned with the effects of different methods of plantation thinning on insect attack on the residual stand. There are three thinning methods being tested in New York State forests. By these methods, unwanted trees are axe-felled, axe-girdled or poisoned. In all three, the unwanted trees are left in the forests, thus eliminating the expense of removal. Such conditions provide potential breeding material for bark beetles and borers, some of which, if present in large numbers, may attack and kill the desirable trees. Each of the thinning methods varies the amount of potential breeding material available at one time. Also, each method varies in cost.

Plots have been laid out in each of ten forest districts which are doing silvicultural work in state reforestation areas (see P in Fig. 1). Several thousand acres of white pine, red pine and spruce will be thinned periodically. Up to the end of July, 1956, over 50 study plots had been laid out in thinned stands in the 10 forest districts. Results of these studies will not be known immediately, although it is known that *Ips pini* (Say), a bark beetle capable of killing live trees, is present in all plots established so far. In some districts it killed many trees in 1955. It is planned to make periodic observations in the study plots over a period of at least five years.

Although we have taken no systematic data as yet, it appears that trees that have been poisoned with sodium arsenite are not attacked so readily as axe-felled trees. The bark becomes brown and dry, and apparently unsuitable for insect attack when trees are poisoned during the growing season.

INSECT DAMAGE AND ITS PREVENTION IN WINDTHROWN SAW TIMBER. A severe windstorm on November 25, 1950, which resulted in heavy blowdown of timber on 343,000 acres in the Adirondacks produced several critical forest insect problems, especially those related to the salvage operations which were carried on for the ensuing three years. The investigations which were thus precipitated were continued for several years, since they related not only to salvage of windthrown timber but also to the increasingly prevalent routine practice of cutting and decking logs throughout the spring and summer, when they will be subject to insect attack. The studies were carried on along several lines, namely, (1) ecological studies to determine the species of insects which attacked the down timber, and (2) control studies to determine whether large scale insect build-up and attack could be reduced; (3) observations especially relating to the activities of the more common woodboring insects and the extent to which their attack affected the salvability of logs; and (4) studies in the sawmills as the salvaged wood was cut into boards, to evaluate the insect damage in the cut lumber and correlate it with data from the superficial observations, in order to develop a sampling method whereby superficial examination would give a more reliable salvability index.

Large scale control tests against insect attack by airplane spraying with 4 lbs. of DDT and .4 lb. of gamma BHC per acre did not reduce attack on windthrown timber. Results of these tests and others are published in the April 1953 issue of the *Journal of Economic Entomology*.

The mill studies of cut lumber showed a direct correlation between the number of insect entries into the wood from log surfaces and the amount of damage occurring in



cut lumber. The greater the intensity of attack, the greater was the damaged volume by both ambrosia beetles and borers, not only because of a greater number of holes in the boards affected, but also because the more holes there were, the greater chance of deeper penetration.

Insect attack on down timber was primarily by ambrosia beetles (Scolytidae) and round-headed borers (Cerambycidae). The principal species which attacked soft woods were the ambrosia beetles, *Trypodendron bivittatum* (Kby.) and *Gnathotrichus materiarius* (Fitch), and the borers, *Tetropium cinnamopterum* Kby. and two species of *Monochamus*. Except for *Monochamus* which penetrated 4 to 7 inches into the wood, most penetration was 2 to 3 inches. The hardwoods were attacked by the ambrosia beetles, *Xyloterinus politus* (Say) and *Monarthrum mali* (Fitch). Attack by the former was more serious and penetrated the wood generally to 3 inches but was often found at a depth of 4 to 5 inches. There was some borer attack but most of it was inconsequential.

Comparison of mill study data on various tree species involved in the blowdown indicated that the differences in relationship between entries and damaged volume are sufficient among the tree species to make it misleading to attempt to predict from data on one tree species what could be expected in the other species, especially when they were attacked by different insects. From the studies, the following factors appear to be most important in determining how much cut volume from a log may be expected to contain insect damage and to what extent: (1) the species of insect attacking; (2) the intensity of insect attack; (3) the diameter of the log; (4) the technique used in cutting the log into lumber. It is therefore important for log graders and scalers to become familiar with the insects and damage occurring in a given logging area and the depths in the wood at which the damage is found. Damage can be culled or logs graded on the basis of type of damage, intensity of attack and the rules regarding exterior defects.

Log spray experiments (see B in Fig. 1) indicated that it is easier to prevent insect attack than to kill the insects after they have entered. Of the insecticide formulations tested, 12 percent DDT in kerosene applied by hand sprayer as a full coverage spray to uninfested logs prevented insect attack for more than a year.

In a mill yard where decks of yellow birch (*Betula lutea* Michx.) logs were kept wet by a water sprinkler to prevent dry rot, there was less attack by the round-headed borer, *Xylotrechus colonus* (Fab.) on the sprinkled logs than on logs not sprinkled.

OTHER INSECTS. Studies on the gypsy moth, *Porthetria dispar* (L.), are being carried on in 12 one-acre study plots in the Lake George area (No. 9 in Fig. 1). The studies involve the correlation of egg deposit with defoliation in different forest compositions and under various site conditions.

The European pine shoot moth, *Rhyacionia buoliana* (Schiff.) has caused considerable damage to red pine plantings in the southern half of the state. Airplane spray tests with 4 lbs. of DDT per acre failed to give consistent control of this pest (No. 10 in Fig. 1). Further tests with airplane sprays are being continued.

In the above paragraphs we have selected for discussion only those insects which have caused the greatest concern or which would seem to have the greatest general interest. Other forest insects which are currently the subject of research by the New York State Science Service and Conservation Department include the beech scale *Cryptococcus fagi* (Baer), *Matsucoccus* scale *M. resinosae* (Bean & Godwin) on red pine, the birch leaf miner *Fenusa pusilla* (Lep.), the saddled prominent *Heterocampa guttivitta* (Wlk.), and the pine leaf aphid *Pineus pinifoliae* (Fitch).

## DISCUSSION

J. D. BLETCHLY. Have the spray treatments against ambrosia beetles included tests with BHC and dieldrin and if so how do they compare with the DDT tests?

D. P. CONNOLA. The spray treatments against ambrosia beetles did not include dieldrin and BHC but did include lindane, 1.25% in kerosene. Results with the lindane were not so good as with 12% DDT which prevented attack by ambrosia beetles up to the time the logs were examined, 15 months after treatment.

J. D. BLETCHLY. Is there any record of *Lyctus* attack in birch as unconfirmed reports of such damage have been received in the United Kingdom from Canada?

D. P. CONNOLA. There were no observations of attack by *Lyctus* on birch studied in this report.

J. D. BLETCHLY. What information is available on the occurrence and importance of the cerambycid *Sarosesthes* (*Arhopalus*) *fulminans*? Recent instance of attack by this insect has been seen in the United Kingdom in infested American white oak.

D. P. CONNOLA. In limited observations on white oak, *Sarosesthes* (*Arhopalus*) *fulminans* was not encountered. However, the species occurs generally in oak in eastern United States and can cause considerable damage.

V. BUTOVITSCH. How deep do the tunnels of *Monochamus* spp. penetrate into the stems and has any association between *Monochamus* attacks and blue stains been observed?

D. P. CONNOLA. We have found in our studies that *Monochamus* spp. tunnels penetrate 4 to 7 inches as measured from the log surface to the greatest depth. We have not noted any particular association between *Monochamus* attacks and blue stains.

R. E. BALCH. Was the relationship between site and white pine weevil damage a matter of rate of growth — that is height and diameter of leaders?

D. P. CONNOLA. Although there appeared to be a correlation with growth, that is trees growing on heavier soils appeared to have a lesser growth rate, we did not measure this factor directly but rather concentrated our observations on the relationships between soil factors and weevil damage.

# Environmental Factors Associated with Outbreaks by the Western Pine Beetle and the California Five-Spined Pine Engraver in California

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## ABSTRACT

*Timber mortality in ponderosa pine due to the western pine beetle and the five-spined engraver fluctuates widely. Studies conducted in northern California between 1939 and 1951 indicate that these fluctuations are influenced by certain environmental factors affecting the timber stand. Timber losses caused by the western pine beetle were significantly associated with precipitation during the spring, soil moisture in mid-July, and average daily temperature from April through July. Outbreaks of the California five-spined engraver appeared to be predominantly influenced by accumulated precipitation deficiencies from April to July and the amount of breeding material left on logged areas cut in the spring of the year. It appears possible to use the combined factors of air temperature, precipitation, and soil moisture to predict losses caused by the western pine beetle, and the factor of deficient precipitation from April to July to predict outbreaks by the California five-spined engraver. Avoiding spring logging or cleaning up logging slash promptly are advisable to check engraver-caused losses.*

## INTRODUCTION

The western pine beetle, *Dendroctonus brevicomis* Lec., and the California five-spined engraver, *Ips confusus* (Lec.), are two of the most destructive forest insects in California. On the average these two bark beetles kill well over 250 million board-feet of ponderosa pine each year. The volume of timber killed fluctuates widely from year to year. These fluctuations are believed to be associated with changes in certain environmental factors affecting the forest stand. To test this hypothesis, studies of bark-beetle-caused mortality in relation to precipitation, temperature, and soil moisture were conducted in a ponderosa pine area near Burney, Shasta County, California, between 1939 and 1951.

The study had two distinct phases. One dealt with the association of various environmental factors with so-called insect hazard zones; the other dealt with the association of some of these same factors with annual fluctuations in insect-caused timber mortality. This paper presents the results of the latter phase of the study and points out the possibility of using certain environmental factors as a basis for predicting annual timber losses caused by the two insects.

## METHOD OF STUDY

The study was set up to obtain data on climatic and other ecological factors in four of the five insect-hazard zones for northeastern California pine stands, as classified by Miller *et al.* (1951). The term "hazard" is used to designate the probability of insect-caused losses. "Zones" designates areas. Recent losses and the volume of high-risk trees in the stand are the basis for rating forest areas according to hazard. ("Risk" refers to the susceptibility of individual trees to bark-beetle attack.) Five degrees of hazard were recognized, ranging from I (Very low), through II (Low), III (Moderate), IV (High), to V (Very high).

A weather station was established in each of four different hazard zones to measure climatic factors during the growing season and the period of insect activity. In addition, a master weather station was maintained at the Hat Creek Field Laboratory all year. The weather stations were designated as follows: Warner Bridge in Hazard V, Blue Lake in Hazard IV, Burney Flat in Hazard III, and Cornaz Lake in Hazard II. The Hat Creek Field Laboratory master station was in Hazard IV. All were at approximately 3,000 feet above sea level except Cornaz Lake, which was at 4,600 feet.

Timber mortality was measured annually on 38 permanent 20-acre sample plots scattered throughout the study area. These plots were supplemented by a series of roadside strips traversing each hazard zone.

### PRINCIPAL INSECT SPECIES STUDIED

The two principal insect species studied are in many respects dissimilar, but they frequently are associated.

**WESTERN PINE BEETLE:** The western pine beetle is primarily a killer of mature and overmature ponderosa pine. Its work is normally confined to the lower two-thirds of the bole and rarely appears in the top part. Normally it breeds in decadent or high-risk trees, such as those with thin crowns, sparse foliage, or other crown weakness, and in trees recently killed by lightning or topkilled by engravers. During epidemics it often attacks and kills thrifty low-risk trees. In the Burney area there are usually three generations per year.

**CALIFORNIA FIVE-SPINED ENGRAVER:** The California five-spined engraver is primarily a killer of young, thrifty-appearing trees which many times are the fastest growing trees in a stand. Attack starts in the top of the tree, and trees under 12 inches in diameter are usually killed. In larger trees, only the top is killed unless the basal part is later attacked by the western pine beetle, as often happens. This beetle, too, usually produces three generations a year in the Burney area.

One very distinct difference is that, while the western pine beetle attacks and kills trees in every generation, the California five-spined engraver practically never attacks living trees during the first summer generation. Instead, this generation is spent in logging residue, broken tops, windfalls, or tops of trees killed by the western pine beetle.

**THE STUDY AREA:** The study area included about 250,000 timbered acres in southeastern Shasta County. Ponderosa and Jeffrey pine made up more than half of the timber volume. The rest was made up of the following species, in descending order of abundance: white fir, sugar pine, incense-cedar, Douglas-fir, lodgepole pine, and red fir. Timber types ranged from those very tolerant of dry-site conditions to those very exacting in moisture requirements.

The precipitation pattern is seasonal in the Burney area, as in most of the ponderosa pine type. About 80 per cent of the total precipitation falls during the 6 winter months. Most falls as snow, which often persists at high altitudes well into the summer months. The summer months are characterized by usually clear and bright days with low humidity and moderately high temperature. There is practically no summer rain except from scattered, local thunderstorms. Wind movement is generally persistent from the south and, while rarely strong, is nevertheless prevalent throughout the day with little movement at night.

**ASSOCIATION OF ENVIRONMENTAL FACTORS WITH LOSS:** Precipitation, air temperature, and soil moisture at the 9-inch depth were all found to be associated with timber loss. Each of these factors was screened by monthly intervals and combinations of months to find the month or combination of months which gave the highest simple correlation with annual loss:

**SIMPLE CORRELATION:** The factors showing the highest simple correlation with annual loss were: average daily temperature in degrees F., April through July, of the year in which the loss occurred; total precipitation in inches for the same period; and soil moisture in per cent for mid-July. These are listed below:

Factor	Simple correlation coefficient	Standard error of estimate %	Significance
Average daily temperature in degrees F., April through July	+ 0.8894	19.2	Highly significant
Total precipitation in inches, April through July	- 0.8677	17.0	Highly significant
Soil moisture in per cent, mid-July, 9-inch depth	- 0.9237	15.4	Highly significant

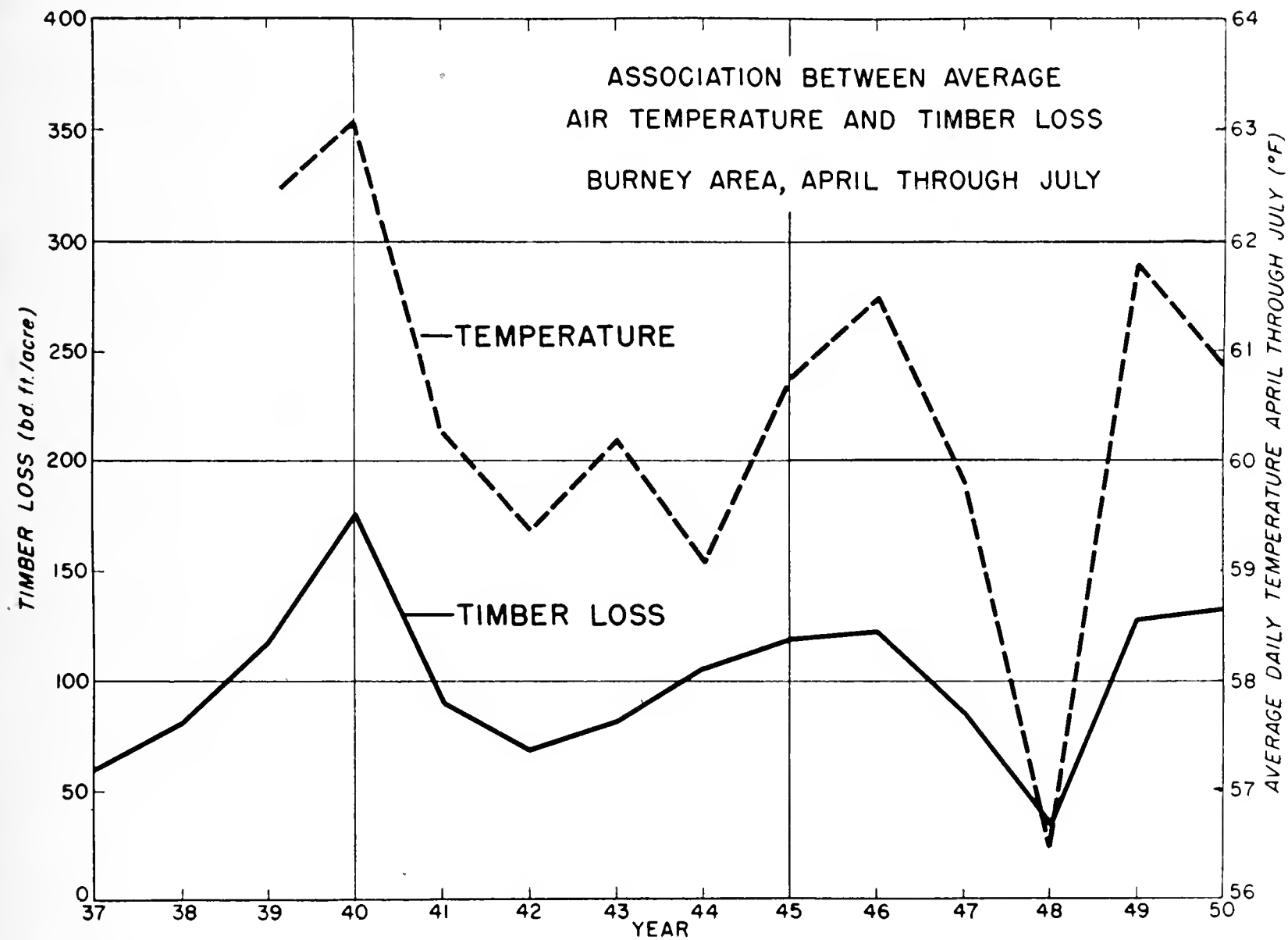
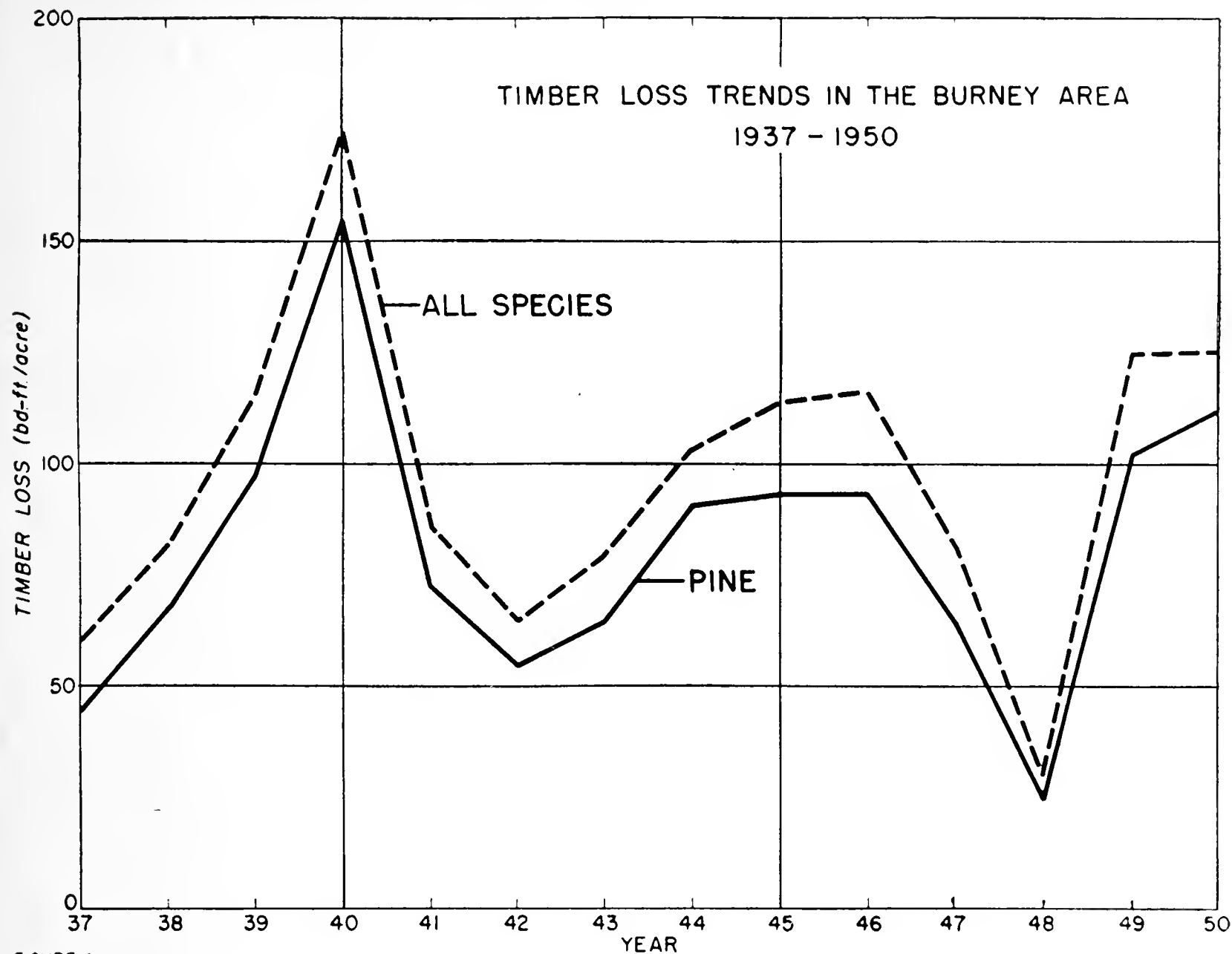


Fig. 1. Timber loss trends in the Burney area, 1937-1950.

Fig. 2. Association between average air temperature and timber loss, Burney area, April through July.



All of the simple correlation coefficients were highly significant. During the period of the study, the losses ranged from a high of 174 board-feet per acre in 1940 to a low of 28 board-feet per acre in 1948 (Fig. 1). The average for the 11-year period was 101 board-feet per acre per year.

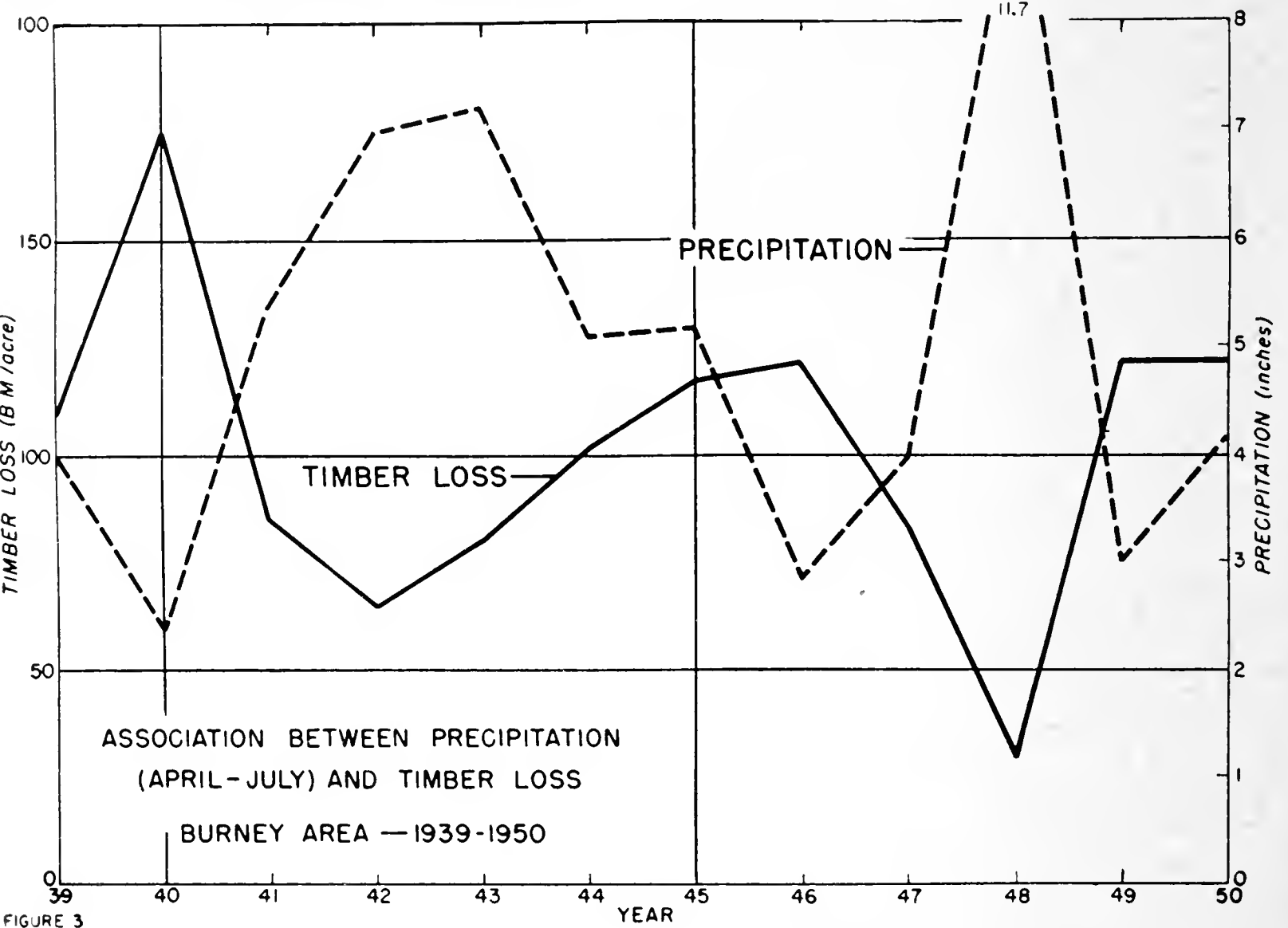


FIGURE 3

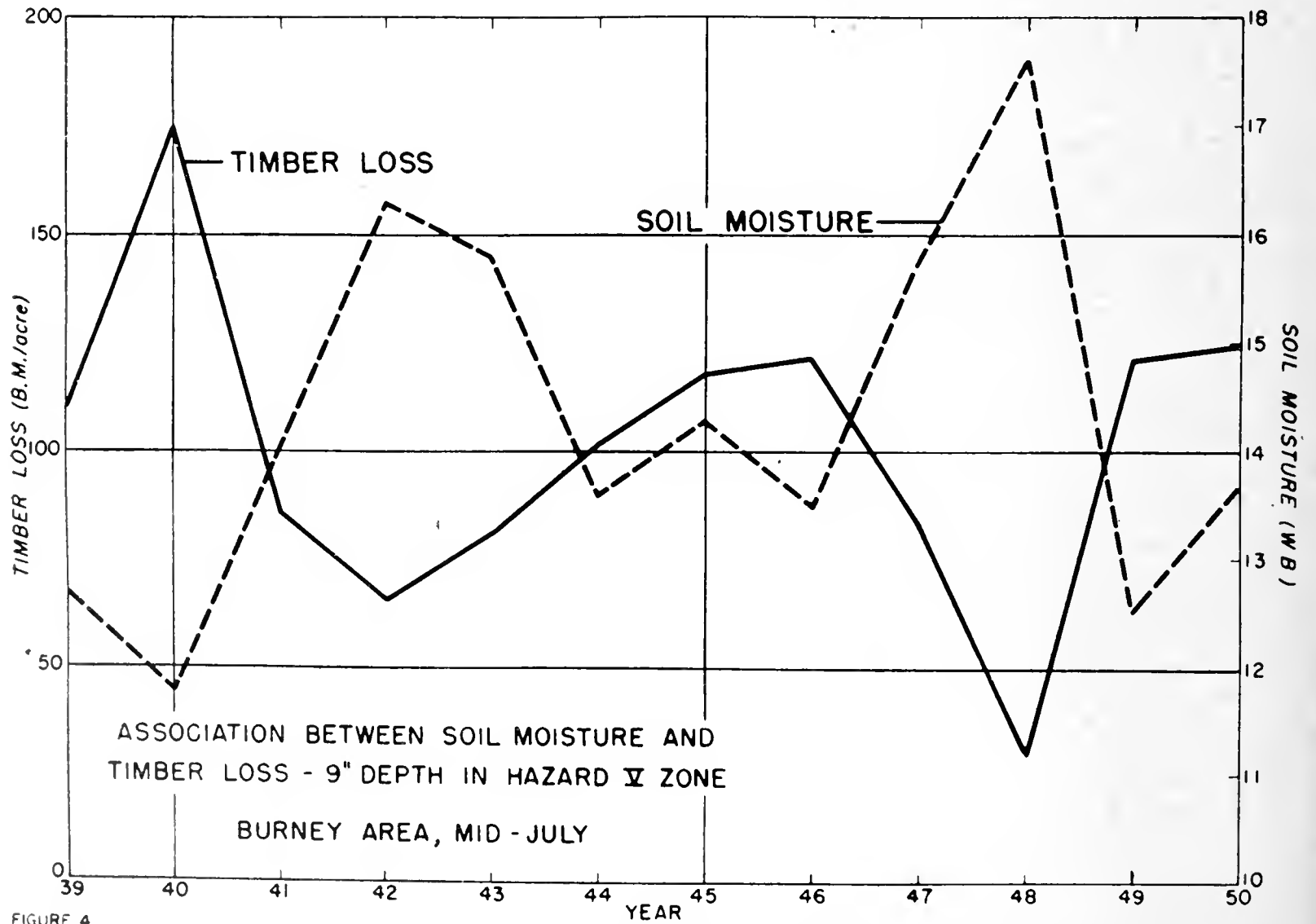


FIGURE 4

Fig. 3. Association between precipitation (April-July) and timber loss, Burney area, 1939-1950. Fig. 4. Association between soil moisture and timber loss; 9-inch depth in hazard V zone, Burney area, mid-July.

The correlation coefficient between average daily air temperature in degrees F., from April through July, and annual loss was positive. In general, higher temperatures were associated with higher losses and lower temperatures with lower losses. In 1940, when the loss was the maximum of 174 board-feet, daily air temperature was highest — 63.1 degrees F. The year of lowest loss — 28 board-feet per acre — was the year of minimum daily temperature — 56.5 degrees F. (Figs. 2 and 5-C).

Total precipitation from April through July was negatively correlated with annual loss. As precipitation increased, losses generally tended to be lower (Figs. 3 and 5-A). In 1940, the year of highest loss, precipitation was at a minimum of 2.4 inches, and the year of lowest loss, 1948, the year of maximum precipitation, 11.7 inches.

Soil moisture at the 9-inch depth at the Hazard V station also was negatively correlated with loss; the tendency was for increasing losses with decreasing soil moisture (Figs. 4 and 5-B). The highest loss came in the year with the lowest soil moisture, 11.8 per cent at mid-July. The wilting percentage of the soil had been determined as 12.6 per cent, and therefore 11.8 per cent represented a very critical situation. When the loss was lowest, the soil moisture was 17.7 per cent, the highest measured during the 12-year period.

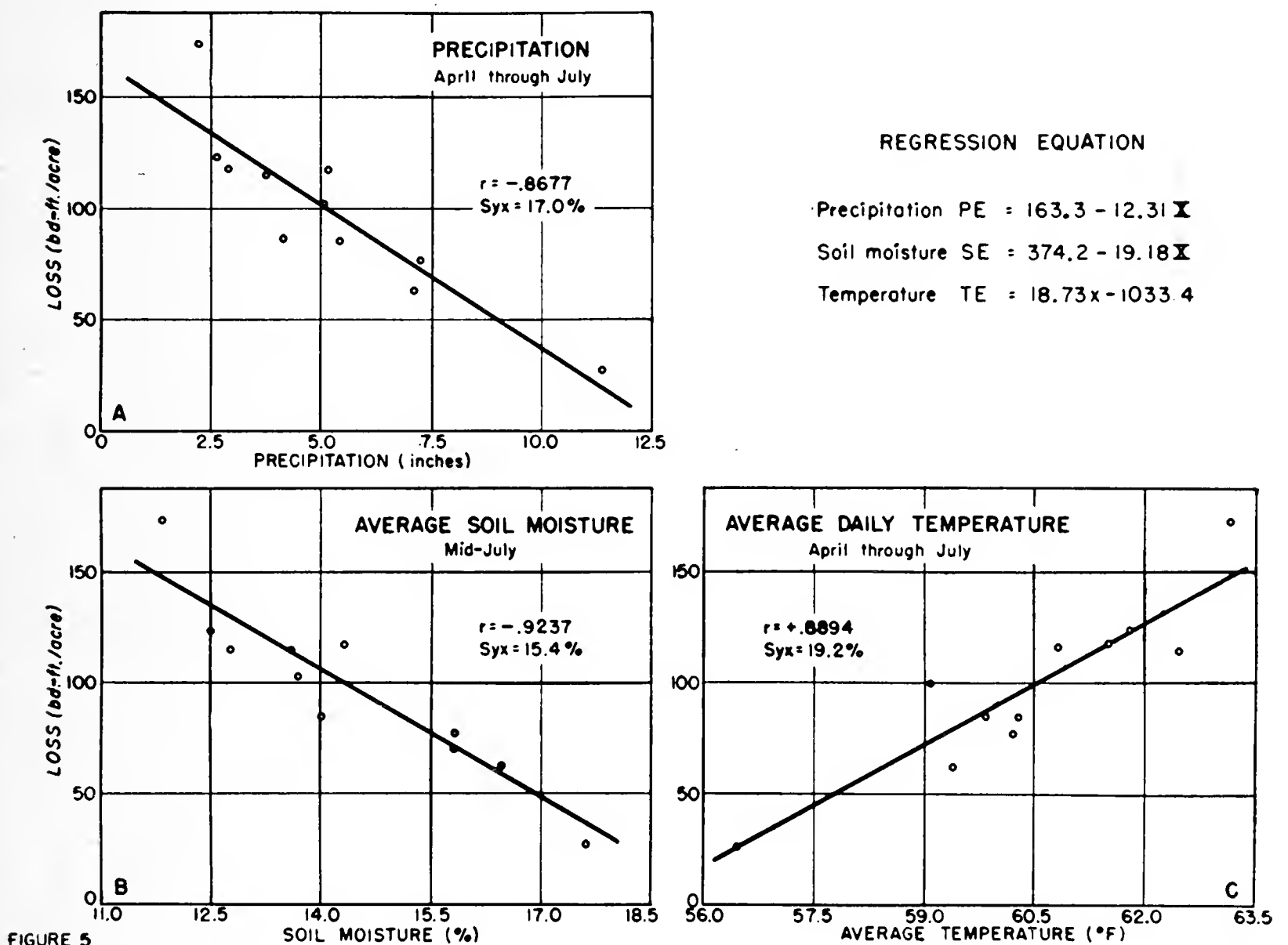


Fig. 5. Regression of precipitation (A), soil moisture (B), and daily temperature (C), with average annual timber loss.

Those factors showing highly significant, simple correlation coefficients were then selected for multiple correlation analyses.

**FUTURE LOSS RELATED TO AIR TEMPERATURE, PRECIPITATION, AND SOIL MOISTURE:** In the multiple correlation analysis the dependent variable Y (future loss) was the average annual timber loss from sample plots, expressed in board-feet per acre. The independent variables were:  $X_1$ , the average daily temperature in degrees F., April through July, at the Hat Creek Master Station;  $X_2$ , the total precipitation in inches at the same station; and  $X_3$ , soil moisture in per cent from the Hazard V station in mid-July.

The multiple correlation coefficient was found to be  $R = +0.9403$ , which was highly significant.

The multiple regression equation for estimating future loss was found to be:  $Y = 5.3265X_1 - 2.4430X_2 - 11.7734X_3 - 39.88$ . The standard error of estimate was 14.56 per cent.

During the 12-year period the maximum percentage error of estimate was 21.5 per cent in 1941 (Table I); the minimum was 0.1 per cent in 1947; and the average for the period, 14.56 per cent.

TABLE I — Average Daily Temperature, Precipitation, Soil Moisture, and Annual Timber Loss, Burney Area, California, 1939 to 1950.

	Average daily temperature $X_1$	Precipitation $X_2$	Soil moisture $X_3$	Actual timber loss $Y$	Estimated timber loss, all species $E$	Error of estimate	
Year	° F.	In.	Pct.	Bd.-Ft./A.	Bd.-Ft./A.	Bd.-ft.	Pct.
1939	62.5	4.0	12.7	115	133.7	+18.7	16.2
1940	63.1	2.4	11.8	174	151.4	—22.6	13.0
1941	60.3	5.4	14.0	85	103.3	+18.3	21.5
1942	59.4	7.0	16.3	64	67.5	+ 3.5	5.5
1943	60.2	7.2	15.8	78	77.2	— 0.8	1.0
1944	59.1	5.1	13.8	101	100.0	— 1.0	1.0
1945	60.8	5.2	14.3	117	102.9	—14.1	12.1
1946	61.5	2.9	13.5	118	121.7	+ 3.7	3.1
1947	59.8	3.9	15.8	83	83.1	+ 0.1	0.1
1948	56.5	11.7	17.7	28	24.1	— 3.9	13.9
1949	61.8	2.8	12.5	124	135.3	+11.3	9.1
1950	60.7	4.3	13.6	126	112.8	—13.2	10.5
Average	60.48	5.16	14.32	101.08	101.08	14.72	14.56

The multiple correlation coefficient of  $+0.9403$  is only slightly better than the simple correlation coefficient of  $-0.9237$  for soil moisture at mid-July. Likewise, the standard error of estimate for the multiple regression coefficient was 14.6 per cent compared with 15.4 for the standard error of estimate for the simple regression coefficient for soil moisture and annual timber loss. Therefore, for all practical purposes, the single factor of soil moisture at mid-July could be used to predict future loss with considerable confidence.

The western pine beetle caused most of these losses, although the five-spined engraver played a dominant role in certain years. Since loss was measured in terms of board-feet per acre, many trees killed by engravers were not included because they were below the merchantable 12-inch diameter class. From 1944 to 1947, however, the engraver killed the tops of many merchantable trees that were later attacked by the western pine beetle and fell into the merchantable-loss sample. Starting in 1944, particular attention was given to engraver attacks.

In general, many of the factors associated with the western pine beetle seemed equally associated with damage by the pine engraver in the Burney area. Two factors in particular, precipitation between April through July and soil moisture at mid-July, appeared to be dominant. Another important factor was the presence of breeding material in the form of logging debris created by cutting operations during the spring months. Losses caused by the two beetles differed in one striking aspect: in certain years the five-spined engraver caused essentially no tree killing in the whole Burney area, but the western pine beetle always killed an appreciable number and volume of trees.

It was difficult to develop a formula for predicting loss from the engraver beetle in terms of a simple or multiple correlation or regression. Sampling the dependent variable — number of trees killed by engravers — was practically impossible. Infestations were very spotty. Often, several thousand acres had not a single engraver-infested tree, but then a single acre might have 100 or more infested trees. Therefore, engraver infestations were considered in four categories of none or very light, medium, and heavy.

Since 1949, the per cent of normal precipitation from April through July has been used to predict the degree of damage from the pine engraver likely to occur in the fall of the year. The basis for prediction has been as follows: 150 per cent or greater precipitation — no appreciable loss; 100 to 150 per cent — light loss; 75 to 100 per cent — medium loss; and less than 75 per cent — heavy loss. In 1949 and 1950, loss was predicted on 20 separate logging areas in 10 counties in northern California. Out of the 40 predictions, 31 were essentially correct, 4 were slightly less than predicted, and 5 heavier than predicted. Since 1950, only general predictions have been made statewide. These annual predictions have been about 75 per cent correct. Discrepancies have occurred during years of about normal precipitation, but predictions have been fairly accurate at the extremes of 150 per cent and greater and 50 per cent. These experiences indicate that per cent of normal precipitation from April through July can be a useful tool in forecasting the degree of five-spined engraver damage in northern California.

#### REFERENCE

- Miller, J. M., K. A. Salman, and P. C. Johnson. 1951. Bark-beetle hazards in the pine stands of northeastern California. Part II. U. S. Dept. Agric., Forest Insect Laboratory, Berkeley, California. 277 pp. (Processed).





# *Eupterote mollifera* and Host Specificity

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Drum stick, *Moringa pterygospermum*, is a tree, the fruits of which are used as vegetables. Drum stick trees usually grow wild and in a few cases are planted in back yards.

*Moringa* is attacked by very few insects, and the most important one is the hairy caterpillar, *Eupterote mollifera* (Eupterotidae). The dirty grey brown-haired caterpillars feed on leaves and completely defoliate the trees. The caterpillars feed during the night and gather around the shoots and stems during the day. As the caterpillars advance in age they come nearer the stem and the earth for rest during the day. They gather in thousands on the bark and the shoots and do not stir at all during the day. It has been observed that the caterpillars begin to move towards the top shoots for feeding as soon as the sun sets and return to the shoots or trunks before the sun rises and the day breaks. It has been also observed that caterpillars do not feed during day even when they are confined in darkness.

Drum stick caterpillars not only defoliate but are a nuisance in the premises of the houses. They are covered with tufts of poisonous hairs which when contacted irritate the skin and cause a severe itch. When caterpillars grow older and are ready to pupate, they move and wander about for pupation in secluded places, cracks and crevices.

So far *Eupterote mollifera* is known to be a specific pest of *Moringa*. But the author found it feeding on some other plants. To find out the host range, plants growing near *Moringa* trees were fed to second instar caterpillars in the laboratory. The leaves of the following plants were used as food: Drum stick, *Moringa pterygospermum* Rath ki rani, *Cestrum aurantiacum* (Solanaceae); Din ka raja, *Citharexylum suberratum* (Verbinaceae); *Duranta*, *Duranta plumeri*; *Acalypha indica* (Euphorbiaceae); *Bougainvillea spectabilis* (Nyctaginaceae). The food was changed every day. The caterpillars, in addition to their specific host fed on *Duranta plumeri*, *Acalypha indica* and *Citharexylum suberratum*. Caterpillars on leaves of *Cestrum aurantiacum* and *Bougainvillea spectabilis* died after about 8 days as they did not feed on the leaves.

The duration of the larval period on the different hosts on which the caterpillars were bred did not vary greatly. The following larval periods were obtained for the different hosts: *Moringa*, 31-33 days; *Duranta*, 34-36 days; *Citharexylum*, 35-40 days and *Acalypha*, 39-41 days. The feeding on *Citharexylum* and *Acalypha* was good. None of the hosts other than *Moringa* are vegetables but are ornamentals.

The control of the pest is a problem as it is found on individual scattered trees. However, among the insecticides, kerosene soap emulsion is the best. The caterpillars can be easily collected when they gather at the trunk and can be burnt or immersed in kerosene.

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# Predation of Sawflies by Small Mammals

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## ABSTRACT

The principles and effectiveness of predation have been demonstrated in studies of the roles of small mammals as predators of *Neodiprion sertifer* (Geoff.), *N. americanus banksianae* (Rohwer), and *N. lecontei* (Fitch). The discussion is confined to the problem involving *N. sertifer*. Predation was restricted to the cocoon stage of the insect. Only three species of small mammals were important predators — *Sorex cinereus cinereus* (Kerr), *Blarina brevicauda talpoides* (Gapper), and *Peromyscus maniculatus bairdii* (Hoy and Kennicott). Prey density and predator density were the only important factors affecting predation. Changes in prey density caused changes in the consumption of cocoons per predators (the functional response) and changes in the density of the predators (the numerical response). These responses differed for the three different predators. The relation between per cent predation and prey density resulted from a combination of the two basic responses. With each predator the per cent predation increased initially with prey increases, and decreased subsequently. The prey density at which predation was greatest increased from *Blarina* through *Sorex* to *Peromyscus*. The maximum predation increased from *Peromyscus* through *Blarina* to *Sorex*.

The functional and numerical responses are the fundamentals of predation. But other subsidiary factors can exert an effect through these basic responses. Prey reactions, by altering the strength of stimulus emanating from prey, changed the functional responses of caged *Peromyscus*. Similarly, increase in the number or palatability of alternate foods decreased the functional response. Such an increase could also increase the density of predators.



# Mammalian Predators of the Larch Sawfly in Eastern Manitoba<sup>1,2</sup>

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## ABSTRACT

The small mammal species frequenting sawfly-infested tamarack stands are listed. It was found that 12 species feed upon cocoons of this insect in a confined universe. Of these, *Sorex cinereus*, the cinereous shrew, *S. arcticus*, the saddle-backed shrew, *Clethrionomys gapperi*, the red-backed vole, and *Microtus pennsylvanicus*, the meadow vole, are probably the most important mammalian predators because these species maintain substantial populations in tamarack bogs. Laboratory studies indicate that these four species reject dead cocoons and cocoons attacked by a fungus. Also, *S. cinereus* and *C. gapperi* reject cocoons parasitized by the tachinid, *Bessa harveyi*, to some extent. Predation under field conditions was estimated by using the "cocoon planting" technique. Although the insect spends a large portion of the year within a cocoon in the soil, most of the predation is exerted in September and October. This is coincident with the small mammal population peak. Cocoons formed in hummocks of the bog are heavily preyed upon and those formed near the roots of trees are especially vulnerable to small mammal attack. Evidence suggests that the foraging of small mammals for larch sawfly cocoons is exerted uniformly with depth, except where the water table prohibits small mammal activity.

The total cocoon predation ranged from 37 to 98 per cent and was usually over 75 per cent. Shrews destroyed more cocoons than mice, although they were usually outnumbered by mice.

## INTRODUCTION

Small mammals, especially rodents, are usually considered as vermin, and man's endeavours have been historically directed toward discouragement or elimination of small mammal plagues (Elton, 1942). Both mice and shrews have been shown to cause damage to forests by consuming large quantities of tree seeds and destroying seedlings and saplings. Recently however, it has been suggested by Graham (1928) and Hamilton and Cook (1940) that these animals are not entirely detrimental to our forest economy and that they may be doing considerable service for us by destroying noxious insects. It has been mentioned (Buckner, 1955b) that predation of forest insects by small mammals is greatest where the insect spends a portion of its life cycle in the forest floor. Most sawflies meet this condition and it has been suggested that the larch sawfly, *Pristiphora erichsonii* (Htg.), is particularly vulnerable to small mammal predation because it remains within its cocoon in the ground for a large portion of the year.

Small mammal predation of larch sawfly cocoons is a major controlling factor in some outbreaks, having almost exterminated the insect from isolated stands (Graham, 1928). Graham suggests that these animals usually account for about 50 per cent of the total cocoon mortality, and occasionally 100 per cent. Despite their importance, little research has been carried out to determine the full role of mammalian predators of insects.

This paper concerns the effect of mammalian predators on the population of the larch sawfly. Field research was conducted in the Whiteshell Forest Reserve in eastern Manitoba. The study may be subdivided into two phases as follows:

- (1) studies on small mammal populations
- (2) studies on the coactions of mammals and larch sawfly.

The first phase has been presented (Buckner, 1957b) and this report considers only that phase of the study concerning the coaction of small mammals and their insect prey. The investigation included determination of species inhabiting larch sawfly

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<sup>2</sup>Based in part upon a thesis presented to the University of Manitoba, 1954, in partial fulfilment of the degree of M.Sc.



infested stands and the abundance of the various species; species that could be induced to feed upon larch sawfly cocoons; the feeding reaction to various types of cocoons; and predation on the sawfly under natural conditions.

Although experiments involving mammals in small feeding cages provide valuable clues to natural behaviour, they should be treated with some caution. The author has attempted to corroborate information derived from this approach with natural field conditions.

### SMALL MAMMAL SPECIES OF TAMARACK BOGS

The following annotated list of small mammals was made from collections taken in larch sawfly infested tamarack bogs. Subspecific identifications are based on the ranges recorded by Anderson (1946), and those species followed by an asterisk (\*) were verified by Dr. Austin Cameron (Curator of Mammalogy, National Museum, Ottawa) from collections made in the study area.

#### ORDER INSECTIVORA

##### Family Soricidae

*Sorex cinereus cinereus* Kerr.,\* the common cinereous shrew. This is the most common and widespread insectivore of the Canadian boreal forest. It has been taken in low to moderate numbers on all plots studied and reached its highest populations in relatively dense stands with wet floors (Buckner, 1957b). This species has been observed feeding upon larch sawfly cocoons in observation cages. It attacks the cocoons by placing a forefoot on the cocoon and biting off the end and consuming the larval inhabitant. The voracity of the species is illustrated by the following observations. The cinereous shrew has been observed to capture and quickly devour adult tabanids, dragon flies, and with some difficulty to open cocoons and pupae of such large species as *Actias luna* Linn., *Antheraea polyphemus* (Cram.), and unidentified sphingids. On one occasion it was seen by the author to attack and kill an adult wood frog.

*S. arcticus laricorum* Jackson,\* the southern saddle-backed shrew. This species is the second most common insectivore of the study region. It has been taken in low numbers on all plots studied, and in moderate populations in a dense stand with a drying floor. It has been observed feeding upon larch sawfly cocoons and the other prey mentioned for the previous species.

*S. palustris palustris* Richardson,\* the American water shrew. The water shrew was taken only once in tamarack bogs during four years of intensive trapping. It fed upon larch sawfly cocoons in cages, but cannot be considered important because of its low occurrence in the bogs under investigation.

*Microsorex hoyi hoyi* (Baird), the American pigmy shrew. This species has been identified on several occasions from collections in the study region. It resembles *S. cinereus* so closely that it is impossible to differentiate the two without resorting to skull characters. No feeding observations have been made on this species, but presumably it reacts in a manner similar to that of the cinereous shrew.

*Blarina brevicauda manitobensis* Anderson, the Manitoba short-tailed shrew. The short-tailed shrew was recorded only as a single specimen taken in 1952, until nine specimens were taken on each of two plots in 1955. It readily attacks cocoons but can be considered only as a minor predator in the study region because of its low population.

#### ORDER CARNIVORA

##### Family Mustelidae

*Mustela erminea richardsonii* Bonaparte, the Richardson's ermine. This small carnivore has been recorded in moderate numbers on all plots trapped. There is no evidence that this animal feeds upon larch sawfly cocoons but it is important as a predator of small mammals that do feed upon cocoons.

#### ORDER LAGOMORPHA

##### Family Leporidae

*Lepus americanus americanus* Erxleben., the American snowshoe hare. The snowshoe hare occurs in low numbers on one plot. There is no evidence to suggest that it is a cocoon predator.

## ORDER RODENTIA

## Family Sciuridae

*Marmota monax canadensis* (Erxleben), the groundhog. A juvenile groundhog was observed once on one plot. This animal was probably exploring, and there is no evidence that this species is a normal resident of tamarack bogs.

*Citellus tridecemlineatus tridecemlineatus* (Mitchell), the thirteen-striped ground squirrel. This species was observed in tamarack bogs during 1952 in very low numbers. The animal has virtually disappeared from the study region in the succeeding three years.

*Citellus franklinii* (Sabine), Franklin's ground squirrel. Franklin's ground squirrels were observed on one plot in very low numbers. It is probably not a normal resident of tamarack bogs. One animal that was caged with larch sawfly cocoons was observed to consume them whole.

*Tamias striatus griseus* Mearns, the grey eastern chipmunk. This animal occurs in very low numbers throughout the study region, and is found occasionally in the bogs. For feeding behaviour and importance see account of next species.

*Eutamias minimus borealis* (Allen), the northern interior chipmunk. This small chipmunk is common throughout the area and occurs in low numbers in tamarack bogs. It has fed upon larch sawfly cocoons in cages and presumably the previously mentioned species will also open cocoons. Because of the low populations of this and the previous species in tamarack bogs, they are probably not important cocoon predators.

*Tamiasciurus hudsonicus hudsonicus* (Erxleben), the Hudson Bay red squirrel. The red squirrel is common in the study region and occurs in low numbers in the bogs. Presumably this species will feed upon larch sawfly cocoons, but the high level of the water table in sawfly infested bogs is possibly a deterrent to predation.

## Family Cricetidae

*Peromyscus maniculatus bairdii* (Hoy and Kennicot), Baird's white-footed mouse. This species occurs in moderate numbers on the fringes of tamarack bogs. It feeds readily on larch sawfly cocoons, but since it does not penetrate deeply into the bogs, it cannot be considered as an important predator of this insect in the study region. On dry sites this species would undoubtedly be a valuable predator of the larch sawfly.

*Synaptomys cooperi cooperi* Baird, Cooper's lemming mouse. The lemming mouse has been captured several times in the bogs of this region (Buckner, 1957a). Presumably it would feed upon larch sawfly cocoons but its failure to maintain high populations suggests that it is not an important predator in this area.

*Clethrionomys gapperi loringi* (Bailey),\* the plains red-backed vole. This is a common species usually occurring in the drier bogs in this area, where it has been found in moderate populations. It feeds readily on larch sawfly cocoons and hence is an important cocoon predator in the study region. Both forefeet are used to grasp and raise cocoons to the mouth. The subspecific status of this population is questionable in the Whiteshell region since the area is the hub of the clines of possibly three recognized subspecies.

*Microtus pennsylvanicus drummondii* (Audubon and Bachman),\* Drummond's meadow vole. The meadow vole is found in all the bogs studied, and reaches its highest population in open sites. It feeds on larch sawfly cocoons and is an important predator in the study region. Its mode of feeding is similar to that of the red-backed vole.

## Family Zapodidae

*Zapus hudsonius hudsonius* (Zimmermann), the Hudson Bay jumping mouse. This species occurs in low numbers throughout the area. The general remarks accorded *P. maniculatus* may also be applied to this species, except that the population of *Z. hudsonius* does not reach the high levels of its cricetid counterpart.

## PREDATION UNDER LABORATORY CONDITIONS

Hardy (1939), using field collections, has shown that 46 per cent of the cocoons of *Diprion similis* (Htg.) in Poland were opened by small mammals during 1936. He points out that there is often considerable overlapping of control factors, since small mammals will prey upon parasitized and diseased cocoons. He suggests that this

overlapping occurs randomly. Morris (1949), on the other hand, disagrees with this assumption since he has shown that mammals, depending upon their insectivorous nature, can differentiate between sound and unsound cocoons of the European spruce sawfly to varying degrees.

Tests were made using caged mammals to determine to what extent these concepts are applicable to small mammal predation on larch sawfly cocoons. The supply of known cocoon types was obtained by collecting large quantities of fifth instar larvae and rearing them to the cocoon stage. Those larvae harbouring eggs of the tachinid parasite, *Bessa harveyi* (Tnsd.), were reared separately, and constituted the supply of parasitized cocoons. Cocoons produced by unparasitized larvae were divided into two classes, determined by pressing them lightly between the fingers. Those in which the contents felt "hard" were classed as "attacked by fungus". Cocoons that felt pliable were classed as healthy. Frequent checks by dissection indicated that the separation techniques were at least 95 per cent accurate. In preparation for the feeding experiment, cocoons of each type were marked with coloured pigments chosen at random.

Preliminary experiments with the red-backed vole, using cages with about 2 $\frac{1}{4}$  square feet of floor space, indicated that the normal feeding behaviour of this rodent was restricted by the size of the cage. All additional tests were made in cages with about 36 square feet of floor space. The bottom of the cage was covered with about four inches of moist sphagnum moss and an excess of natural food was supplied so that the experimental animals would not be driven by hunger to feed excessively on the sawfly cocoons. The test cocoons were scattered under a layer of moss to simulate natural conditions.

During these experiments the meadow vole opened 72 per cent of the sound cocoons, 67 per cent from which *B. harveyi* had emerged and 19 per cent from which the sawfly had emerged. The red-backed vole opened 73 per cent of the sound cocoons, 79 per cent of the cocoons from which *B. harveyi* had emerged, and 21 per cent of the cocoons from which the sawfly had emerged. The cinereous shrew opened 91 per cent of the sound cocoons, 21 per cent of the cocoons from which *B. harveyi* had emerged, and no cocoons from which the sawfly had emerged. The saddle-backed shrew opened 97 per cent of the sound cocoons, 10 per cent of the cocoons from which *B. harveyi* had emerged, and no cocoons from which the sawfly had emerged. All species unerringly rejected cocoons attacked by fungus. Shrews opened very few cocoons with *B. harveyi* emergence holes, and this was significant at the one per cent level when tested by means of individual 2 x 2 Chi-square tests. These experiments agree with those conducted by Morris (1949) and provide additional evidence that the degree of rejection of unsound cocoons is related to the proportion of insect food in the diet of each species.

Morris suggested that living parasites would probably be as acceptable to small mammal predators as the sawfly itself, but unfortunately he had no source of parasitized material to test this hypothesis. Parasitized cocoons obtained by the author provided a means of testing the validity of Morris' suggestion. Table I lists the results of experiments to determine whether or not the various mammalian species reject cocoons parasitized by *B. harveyi*.

TABLE I — Results of Feeding Experiments to Test the Ability of Small Mammals to Reject Larch Sawfly Cocoons Containing Living Parasites of *Bessa harveyi*.

Species	Type of Cocoon	No. Opened	Total	% Opened
<i>M. pennsylvanicus</i>	Sound	56	78	72*
(2)	Parasitized	9	19	47
<i>C. gapperi</i>	Sound	591	780	77**
(10)	Parasitized	51	190	27
<i>S. cinereus</i>	Sound	1393	1560	89**
(20)	Parasitized	110	380	29
<i>S. arcticus</i>	Sound	1496	1560	96
(20)	Parasitized	349	380	92

\*Difference significant at the 3% level

\*\*Difference significant at the 1% level

Bracketed numbers indicate number of animals tested

This experiment suggests that the red-backed vole and the cinereous shrew reject cocoons containing living *B. harveyi* larvae. The discriminating powers of the meadow vole are doubtful in this respect, and are negligible for the saddle-backed shrew. The selectivity of the red-backed vole and the masked shrew was tested using various percentages of parasitized cocoons. Above 50 per cent parasitism, the percentage of parasitized cocoons opened by the red-backed vole increased, while rejection of parasitized cocoons by the masked shrew remained relatively constant at various levels of parasitism.

An attempt was made to determine the mechanism governing rejection. Two hypotheses were tested, namely that rejection is dependent on the size of the parasite, and that the degree of super-parasitism influences rejection. Accordingly, a series from the parasitized cocoon stock was dissected, the length of the parasite measured, and the degree of super-parasitism recorded. Parasitized cocoons rejected by the red-backed vole and the cinereous shrew were also dissected and the results compared. If one of these factors had been influencing rejection, its frequency would have risen in the rejected cocoons. No significant differences could be found in the sample and rejected cocoons indicated that these factors may not be held responsible for rejection behaviour. Holling (1955) has shown that the size of a parasite of the European pine sawfly influenced the degree of selectivity by small mammals. However, the extremely small size of the parasites used in the present experiment probably preclude degrees of detection.

In attempting rejection experiments, the duration of the trial is important. If the experiment is to yield valid results, the trial should not be extended beyond a period in which starvation causes the experimental animals to feed indiscriminately on the cocoons. During the author's experiments it was concluded that 24 hours in the case of rodents, and 8 hours in the case of the insectivores constitutes a fair trial. This will give an approximate indication of the capacity of each species in destroying cocoons. It appears that the rodents could open about 200 cocoons in a 24-hour period and that the cinereous and saddle-backed shrews could open about 500 and 800 respectively over the same period.

The ability to distinguish cocoons opened by mice from those opened by shrews is important if any degree of accuracy is to be obtained in assessing control of the larch sawfly by small mammals using cocoon analysis. Graham (1929) has suggested that it is possible to determine whether a cocoon of the larch sawfly has been opened by a mouse or by a shrew by examining the opening. Morris (1949) however, has claimed that this is not possible with cocoons of the European spruce sawfly. In order to test this possibility for the larch sawfly, 20 cocoons known to be opened by mice and 10 cocoons known to be opened by shrews from the preceding experiment were examined by 25 independent observers using the criteria that cocoons opened by shrews have serrated edges and often have a cap or "lid" over the opened end. Cocoons opened by mice have scalloped edges. Shrews usually make only one opening in the cocoon, but may make a second opening. Mice however may open a cocoon in three or more places. Fig. 1 illustrates these differences.



Fig. 1. Cocoons of the larch sawfly showing differences in openings made by small mammals. From left to right, a sound cocoon, a cocoon with scalloped edges characteristic of mouse predation, a cocoon with serrated edges characteristic of shrew predation, and a cocoon illustrating the "cap" sometimes left by shrews.



It was found that untrained persons could distinguish cocoons opened by mice with 85 per cent accuracy (with a confidence interval of the mean at the 95 per cent level from 84.54 to 85.46 per cent) and cocoons opened by shrews with 83.6 accuracy (confidence interval of mean 82.81 to 84.39 per cent). Evidence indicates that proficiency in determining cocoons opened by these two mammalian orders may be increased by experience.

### PREDATION UNDER FIELD CONDITIONS

Small mammal predation on larch sawfly cocoons under field conditions was estimated for four years on three plots using a modification of the "cocoon planting technique" employed by Graham (1928). He planted five cocoons per set, all enclosed in a small cotton bag. These were examined at intervals and the percentage of predation recorded.

The present author wired two cocoons about two inches apart on tree tags and these were buried to a depth of about two inches with the top inch projecting from the soil in order to locate the tags during subsequent examinations. One hundred sets were planted on each plot. These were examined at intervals and the individual cocoons recorded as being untouched, attacked by fungus, parasite emerged, opened by a mouse, opened by a shrew, or removed (presumably by a small mammal). Cocoons that were missing or opened were renewed after each examination. The plots studied have been described in some detail (Buckner, 1957b), but brief descriptions follow:

*Plot 1.*—This plot was situated in a mixed stand of tamarack and black spruce about 30 to 40 feet high with a relatively dry floor. The dominant small mammal species was the red-backed vole except in 1954 when the meadow vole was more common. The cinereous shrew was present in low numbers.

*Plot 2.*—This plot was located in a mixed stand of tamarack and black spruce about 12 to 18 feet high. The water table was closer to the surface than that on Plot 1. The meadow vole was the common small mammal species and the cinereous shrew was present in low numbers.

*Plot 3.*—This plot was located in a pure tamarack stand. The trees were about 40 feet in height. The water table was very close to the surface in 1952 and 1953 but fell considerably thereafter because of a drainage operation (Buckner, 1955a). The cinereous shrew was the dominant mammal during the period of high water levels, but appears to have been replaced by the saddle-backed shrew and low numbers of the red-backed vole in the subsequent period.

By using the cocoon planting technique, it was found that small mammals prey upon larch sawfly cocoons during a limited season. It was formerly supposed that this insect was particularly vulnerable to mammalian predation because it remained in the ground for some 10 months of the year, thus affording an extended period in which small mammals could prey upon it. However, it is apparent that light predation begins in August, (or perhaps earlier in some seasons) reaches its greatest intensity during September, and then slowly declines until November (Buckner, 1953). After this, little or no predation occurs on this generation of cocoons. Thus small mammals prey upon the larch sawfly to a limited extent in late August, reach a climax in September, and then slowly relax their predation pressure until the ground is frozen. This constitutes the entire foraging period until the following August when mammalian predators again begin to destroy cocoons. Observations suggest that small mammals prey upon cached cocoons during the winter months. However these have already been removed from the field population, and once cached are potentially destroyed.

The planting technique is also useful in determining the extent of predation in various field situations. It was found that cocoons planted beside the roots of trees and in hummocks in the bogs were heavily preyed upon by small mammals. On the other hand, cocoons in the low lying places between the hummocks were frequently missed by mammalian predators especially when these locations were at or near the water table. These observations have been substantiated by persons collecting cocoons in these situations.



The effect of cocoon depth on predation may also be tested by means of the cocoon planting technique. Accordingly, cocoons were planted at various depths in the moss and the predation assessed. One hundred sets (200 cocoons) were planted at each depth and the results are recorded in Table II. The water table was relatively

TABLE II — Small Mammal Predation at Various Depths as Assessed by the Cocoons Planting Technique.

Depth in Inches	% Predation—Plot 1			% Predation—Plot 2			% Predation—Plot 3		
	M	S	T	M	S	T	M	S	T
2	60	17	77	6	88	94	5	88	93
4	51	7	58	9	77	86	11	79	90
6	69	12	81	4	59	63	9	81	90
8	9	0	9	2	22	24	8	73	81
10	5	1	6	0	0	0	12	74	86
12	14	0	14	0	0	0	9	79	88

M— % opened by mice  
S — % opened by shrews  
T — Total % predation  
Heavy line — approximate depth of water table

close to the ground on Plots 1 and 2 and the extent of predation diminished as the water table was approached. On Plot 3, the water table was considerably deeper, and predation was not influenced by depth. This experiment suggests that small mammals operate uniformly with depth except where the water table prohibits their activities. However, the insect is probably prevented from spinning a cocoon under these conditions, unless the water rises after the cocoons have been formed.

The most important feature of the cocoon planting technique is that it provides a measure of small mammal predation on natural populations of larch sawfly cocoons. Most small mammals leave the opened cocoon on the tag, so it is possible to determine the order of the predator that has opened the cocoon. The results of four years of predation studies are listed in Table III. These data illustrate the importance of small

TABLE III — Percentage of Cocoons Opened by Small Mammals as Determined by the Planting Technique.

Plot	Date	% Opened by Mice	% Opened by Shrews	Total
1	1952	43	14	57
	1953	60	17	77
	1954	14	23	37
	1955	11	43	54
2	1952	28	41	69
	1953	6	88	94
	1954	36	43	79
	1955	22	54	76
3	1952	17	32	49
	1953	9	89	98
	1954	8	78	86
	1955	6	86	92

mammals as predators of the larch sawfly in the study region and emphasize the proportional effect of shrews in reducing the population. The greater intensity of predation by shrews is further emphasized by pointing out that in most cases (with the notable exception of Plot 3), mice outnumber the shrews by at least two to one (Buckner, 1957b).

GENERAL DISCUSSION

The results of this study indicate that small mammals are important natural control agents operating against the larch sawfly in the study region. It has been shown that shrews are especially beneficial in destroying larch sawfly cocoons because of their voracious appetites. In addition, at least one species of shrew and one species of mouse

reject some cocoons containing parasitized larvae. Also, cocoons attacked by fungus organisms were rejected unerringly by all mammalian species tested. Hardy (1939) suggested that small mammal predation encroached randomly onto other natural control factors. This eliminates some of the overlap of various control factors operating against the host insect. The results of this experiment however, coupled with data presented by Morris (1949), indicate that the interaction of other biological control factors and predation by small mammals is considerably less than that suggested by the random concept.

From these experiments it is possible to rate the various mammalian species according to their relative effectiveness as predators of the larch sawfly. The field vole and the red-backed vole have a daily cocoon capacity of about 200. The red-backed vole, however, rejects almost twice as many parasitized cocoons as the meadow vole. Considering a hypothetical case in which parasitism is 50 per cent, the red-backed vole would destroy daily about 140 sound and 60 parasitized cocoons. The field vole in the same situation would destroy about 120 sound and 80 parasitized. The cinereous shrew would destroy 380 sound and 120 parasitized cocoons while the saddle-backed shrew would account for about 400 each of the parasitized and unparasitized cocoons. This reasoning of course makes no attempt to relate searching ability of the various predators, or to account for differences due to varying cocoon or predator densities. It does, however, illustrate the probable superiority of the insectivores as predators, the cinereous shrew from its powers of discrimination and the saddle-backed shrew from its potential cocoon capacity. Since each plot studied has a predominant small mammal species, the effect of each predator can be observed under natural conditions. The effects due to the feeding capacities have already been noted. However, no concrete evidence has been brought forward to show a changing parasite complex in the field due to the rejection behaviour.

This paper has been concerned only with small mammal predation on the cocoons of the larch sawfly. The insect is also vulnerable to predation when it falls from the host tree as a mature larva but before it spins a cocoon. Inadequate data prohibit a discussion of this phase of the study at the present time.

The full importance of mammalian predation upon larch sawfly cocoons will not be realized until the relationship between predator and prey populations and the resultant utilization of the prey insects by the predator is established. Preliminary studies indicate that the rodents do not exhibit any obvious relationship in this respect. This might be expected since rodents are presumably chiefly vegetarian, and their utilization of insect food under these circumstances would be somewhat haphazard. Shrews, being chiefly insectivorous, should show a greater density relationship. This of course would be influenced by the abundance of alternative food supplies, and the minimum sawfly cocoon populations which would support active shrew predation. Investigations on this phase of the problem have been delayed because of inadequacies in the existing cocoon sampling technique. Gross estimates however intimate that there is a clearer relationship between shrew populations, sawfly cocoon populations, and shrew predation than there is with the comparable rodent series.

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### DISCUSSION

M. L. PREBBLE. Has the speaker any evidence that the small mammals feed upon the falling full-fed larvae before spinning of cocoons?

C. H. BUCKNER. Small mammals have been demonstrated to feed upon larvae that have not yet spun cocoons by staking out larvae in a similar manner to cocoon "planting". A small percentage of these were taken. Animals in cages readily fed upon uncocooned larvae, but sawfly remains in stomachs examined during the larval drop period were rare.

C. M. BAETA NEVES. Je veux savoir si dans la détermination des numéros qui font part du tableau III l'auteur a employé des méthodes des statistiques.

C. H. BUCKNER. In the preparation of Table III statistics were not employed, but the data are amenable to statistical analysis and have been analysed by statistical methods in earlier reports.



# The Use of the Host Size and Density Factor in Appraising the Damage Potential of a Plantation Insect

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## ABSTRACT

The Saratoga spittlebug is one of the most important plantation pests in the Lake States. More than 60,000 acres of red pine have been sprayed since 1946 to prevent tree mortality. Tree damage, as measured by spittlebug feeding-scar density on the twigs, cannot be accurately predicted solely on the basis of the insect population. However, if the insect population is adjusted with the tree size and density factor, a simple linear regression of this on resulting tree damage emerges.

The insect population (A) is determined by unit-area sampling during the nymphal stage. Results are expressed in terms of the average number of nymphs per acre. The host size and density factor (B) is expressed as a product of the average tree height (in feet), the average number of branch whorls per tree, and the number of stems per acre. Tree damage (X) is the average number of feeding scars per 10 cm. of the 2-year-old internodes. When X is plotted against  $\frac{A}{B}$ , a straight line of the following type

results:  $X = \frac{A}{B} K$  where:  $K = 17$  (the slope).

The above relationship will hold for different levels of infestations in plantations containing trees of various sizes and densities. It is, therefore, suggested that measuring the spring nymphal population, as well as tree size and density, is an adequate basis for predicting adult Saratoga spittlebug damage and need for control.

## INTRODUCTION

When deciding whether a particular forest insect infestation is in need of artificial control, forest entomologists generally employ a damage appraisal survey. Thus, in the case of the spruce budworm, the criterion for a control operation involves principally the amount of top-killing and the number of consecutive years of heavy defoliation. However, a damage appraisal survey of this type cannot be used for all forest insects. Pests such as the pine tortoise scale and the Saratoga spittlebug (*Aphrophora saratogensis* (Fitch)) do not cause characteristic host damage symptoms in time to allow for the planning and application of a control program before irreparable damage has been done to the trees. In these special cases, the forest entomologist must devise a method of estimating the insect population and predicting the subsequent amount of host damage.

This paper will deal with some of the problems encountered in establishing a host damage prediction system for Saratoga spittlebug infestations in red pine plantations in Wisconsin and Michigan.

## ECONOMIC IMPORTANCE

Severe infestations of the Saratoga spittlebug in red pine and jack pine plantations were first noted in 1940 in northern Wisconsin and Michigan. Twig mortality, top-killing, and whole tree mortality rapidly developed in plantations ranging in height from about 2 to 15 feet. Fortunately, the advent of DDT provided an effective control for this pest and probably prevented the complete loss of plantations in areas containing alternate hosts suitable for the development of the nymphs.

Since 1946, 4,000 to 10,000 acres have been sprayed annually to control the Saratoga spittlebug on Federal land in this section of the Lake States Region. In general, a single operation using 1 pound of DDT in 1 gallon of oil per acre will protect the trees for at least 3 years. The trees are usually out of danger when they



reach a height of about 15 feet since crown closure results in shading-out of the alternate hosts. Also, the larger trees are more tolerant to spittlebug feeding.

### DESCRIPTION, LIFE CYCLE, HABITS, AND HOST DAMAGE

In northern Wisconsin, adults of the Saratoga spittlebug first appear during late June or early July. They are 8 to 10 millimeters long and their color is tan or light brown. The wing covers are irregularly mottled with light spots, and a slightly elevated light stripe is located along the median dorsal line of the head and pronotum.

The adult feeds by inserting its mouth parts through the bark and into the phloem of the young pine twigs causing a typical resin-infiltrated scar. As the season progresses, a necrotic scar also develops in the xylem adjacent to the injured cambium. The cambium is generally healed over by proliferation from the sides by the end of the summer. Occasionally, however, healing does not take place for two or more seasons. This leaves a severe "residual" scar tracing through two or more rings in the xylem. Injury to the tree is brought about by a number of factors associated with feeding of the spittlebug: (1) direct withdrawal of considerable quantities of plant juices, (2) girdling of the phloem by the necrotic feeding scars, (3) plugging of the xylem and subsequent disruption of water conduction, and occasionally (4) the establishing of an associated plant pathogen, the burn blight fungus, *Chilonectria cucurbitula* (Curr.) Sacc.), of which the adult spittlebug is the vector.

About 2 weeks after adult transformation the females begin laying eggs in the buds on the upper portion of the trees. The shiny yellow eggs are about 1 millimeter in length and tear-drop shaped. From 3 to 100 or more eggs can be found under the scales of an infested bud.

The eggs overwinter, and hatch during late May. The nymphs feed and form spittle masses near the root collar of various low-growing plants. Woody plants such as sweetfern and brambles are the preferred alternate hosts; but infestations can develop in areas containing only herbaceous ground cover.

When feeding, the nymphs are generally concealed beneath a layer of ground litter. There are five nymphal instars, each of about 8 days' duration. The first four instars are strikingly characterized by scarlet abdomens and shining black heads and thoraces. The fifth instar is brown or mahogany in overall color, sometimes becoming very dark in the latter part of the stadium.

### DEVELOPMENT OF THE APPRAISAL TECHNIQUE

There is probably a consensus among applied entomologists indicating that insecticides should be used only when serious economic loss is imminent. When appraising Saratoga spittlebug infestations in red pine plantations, the difficulty lies in attempting to differentiate between those infested plantations in danger of serious damage and those which will be able to tolerate the infestations. In the past, attempts have been made to classify empirically the intensity of an infestation by measuring either the nymphal population on a per-alternate-host basis or the adult population on a per-sweep basis. These techniques were expedients developed rapidly to cope with widespread, severe infestations.

Experience has shown that in addition to the insect population, several other factors must be considered in appraising the severity of spittlebug infestations. These are: (1) the density of the alternate hosts, (2) the number of pine hosts per unit area, and (3) the size of the pine hosts. Incorporation of these additional factors can probably be defended to everyone's satisfaction on a theoretical basis. If accurate measurements are found, the aggregate will be a faithful expression of the damage potential of a given spittlebug infestation.

Some quantitative measure of host damage must be found, however, before the appraisal system can be finally drawn. A given spittlebug population can then be correlated with the resulting amount of host damage, and the picture will be complete. Fortunately, Saratoga spittlebug damage may be assessed easily. The feeding scars on the twigs can be counted and used as a direct measure of host damage.

## THE TEST METHOD

To test the feasibility of predicting the amount of tree damage resulting from a given nymphal population, permanent study plots were established in several infested northern Wisconsin red pine plantations. It was decided that the population measurement would be most accurate and useful if carried out during the nymphal stage. There are two reasons for this: (1) measurement of the adult population cannot be conducted in time to set up a control program, and (2) measurement of the egg population not only presents great sampling difficulties but also does not allow for the decimating factors up to the adult stage.

Each study area was a square 1/10 acre subdivided into milacre plots. The nymphal population was measured by counting all the nymphs on 10 systematically located milacre plots. Since a unit of area was sampled, the actual nymphal population was obtained without considering alternate host density.

To determine whether there is any decline in population between the fourth and fifth instar nymphs and the adults, the adult population was also measured. This was done by dropping a large plastic tent over representative trees in the study area and then introducing an insecticide. The adults, which fell on a large muslin base sheet, were counted and the average number obtained was extended to the rest of the trees in the area. The adult population proved to be virtually the same as the mature nymphal population.

Tree damage in the study plots was measured in the fall after the adults had finished feeding. Damage was expressed in terms of the average number of feeding scars per 10 linear centimeters of the 2-year-old internodes.

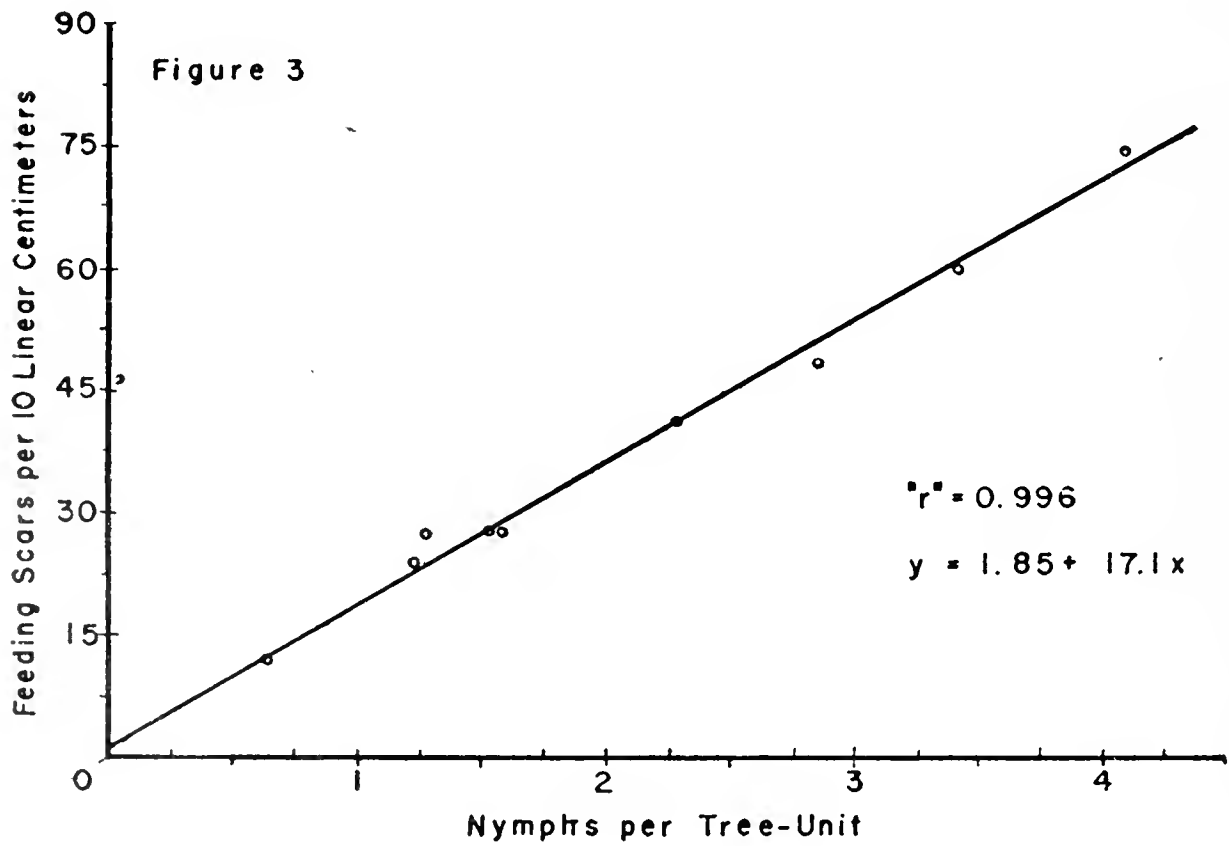
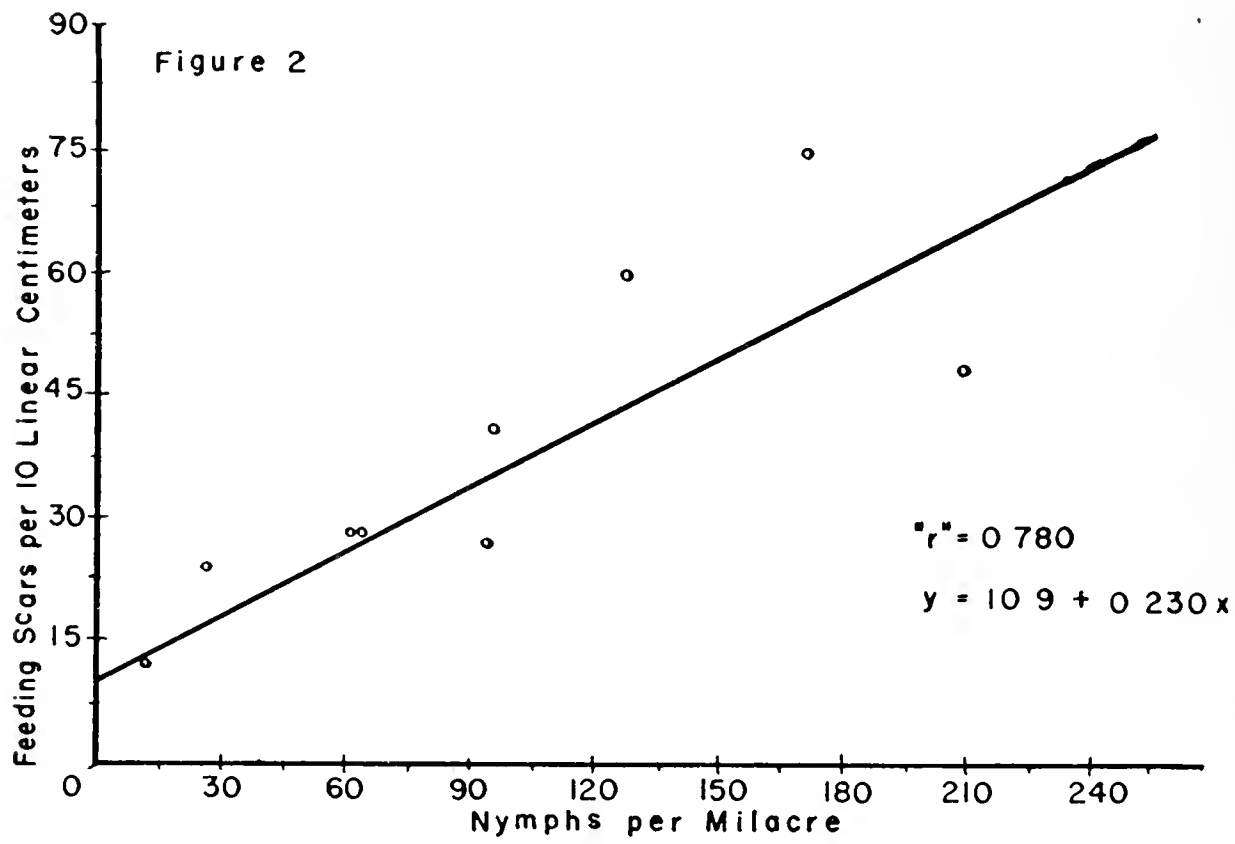
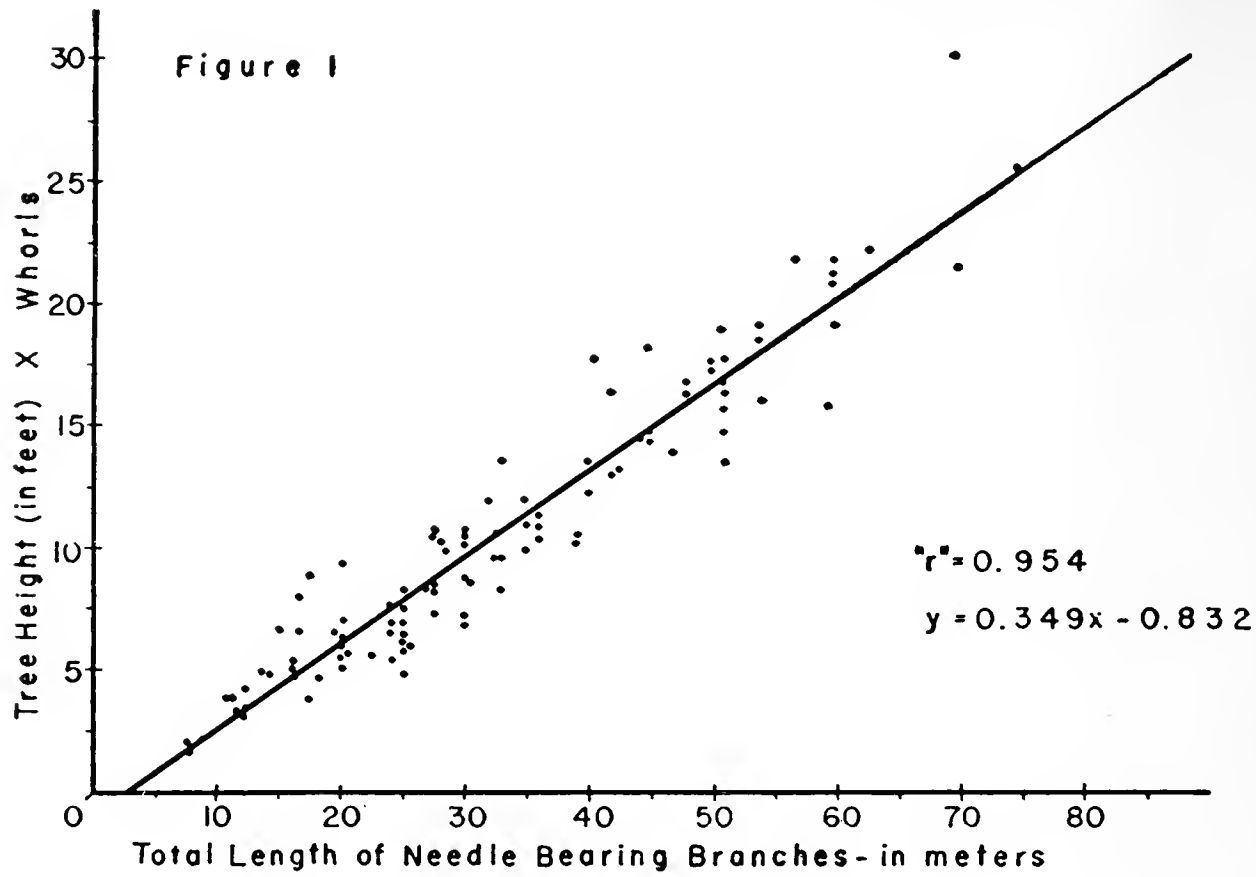
Several methods of expressing the pine host size and density were tested. Since red pine is a symmetrical uninodal tree, it lends itself quite readily to size measurements. Also, since the trees grow in comparatively even rows, the tree density — that is, average number of trees per acre — can easily be measured. The expression finally adopted was the product of the average tree height (in feet), the average number of branch whorls per tree, and the average number of trees per acre. For convenience, this product has been labeled "tree-units" and it represents the total amount of "food" available for the insect population. It was assumed that the number of tree units (which is easily determined) is an accurate expression of the total length of the needle-bearing internodes. This is to be expected because the number of whorls increases with age and consequently with total height. The average length of branch also increases with total height. To verify this assumption, measurements on trees of various heights were correlated. The results showed a very good linear relationship between total length of needle-bearing internodes and the product of tree height and number of whorls (Fig. 1).

Finally, a simple proportion was established between the number of nymphs per tree-unit and the subsequent number of feeding scars in each of the study areas. Tests indicated a good correlation between this proportion and feeding damage in each area.

## THE RESULTS OBTAINED

Data from nine study areas were collected and analyzed. The spittlebug population levels ranged from an average of 13 nymphs per milacre in the lightest infestation to an average of 210 nymphs per milacre in the heaviest infestation. The mean variation of nymphal count within study areas was about 15 percent. The average number of feeding scars per 10 centimeters of the 2-year-old internodes on the areas with the lightest and heaviest infestations were 12 and 75, respectively. Mean variation for the feeding scar counts amounted to about 10 percent within the study areas.

When the nymphal populations per milacre were plotted directly against the feeding scar counts, the correlation was fair (Fig. 2). However, when the nymphal populations were adjusted with the host size and density factor (nymphs per tree-unit), an excellent correlation resulted (Fig. 3). The regression of feeding scar density on the number of nymphs per tree-unit can be taken as a straight line, and the formula for this line is actually a damage prediction system. That is, if the spring nymphal population and the number of tree-units in an infested plantation are known, it is



possible to predict the subsequent amount of tree damage. The amount of feeding predicted will, of course, be the criterion for a control operation. Empirical observations show that if infested trees exhibit 30 or more feeding scars per 10 centimeters of the 2-year-old internodes, twig mortality and growth deterioration will generally occur and the infestation definitely should be slated for control.

According to the equation developed from the data in this study, an average of 1.64 nymphs per tree-unit will produce 30 feeding scars per 10 centimeters.

The accuracy with which this prediction system will work remains to be seen. However, it seems likely that as long as there is no great spittlebug mortality between the time of the nymphal sample and the adult stage, there will be no great margin for error.

### DISCUSSION

D. P. CONNOLA. Have any efforts been made to destroy the alternate host plants by the use of herbicides?

HERBERT G. EWAN. Yes, several attempts have been made to eradicate sweetfern in northern Wisconsin with various herbicides. As far as I know, these attempts have met with absolutely no success.

R. M. BELYEA. How close is the association referred to between the burn-blight fungus and the spittlebug?

HERBERT G. EWAN. Formerly, the burn-blight fungus caused mortality in young spittlebug-infested jack-pine plantations. Currently, the spittlebug is found only in red pine plantations and the fungus is found only very seldom.

J. W. BONGBERG. The procedures developed by Mr. Ewan for evaluating the entomological significance of spittlebug infestations illustrate the close interrelationship of research and surveys in program work by the Division of Forest Insect Research of the Forest Service. The methods used to detect the occurrence of damaging numbers of spittlebugs also illustrate a type of planned detection survey where tree-damage symptoms are not evident.

M. L. PREBBLE. Would you be inclined to rate the importance of control action entirely on the numerical value of  $X$  from the formula, regardless of the number of trees per acre entering into the factor  $B$ ? The smaller the number of trees per acre, other things being equal, the larger would be the value of  $X$  for a given nymphal population density ( $A$ ). Would value of the stand be considered in planning control operations in stands with low tree density but high nymphal populations?

H. G. EWAN. It is true that in the formula,

$$X = \frac{A}{B} K,$$

an economically unrealistic value for  $X$  will be obtained as  $B$  decreases below a certain critical level. It is the policy of the U. S. Forest Service to consider a red pine plantation a failure if less than 400 trees per acre survive. In such plantations, spittlebug control is considered uneconomical regardless of the insect population. The tree-survival level representing the borderline between success and failure — and, consequently, the justification for control action — is an arbitrary thing involving several economic factors. However, even though control is not warranted because of poor survival, from a purely biological standpoint the formula will predict feeding intensity with reasonable accuracy even when the tree density is as low as 150 stems per acre. Undoubtedly, at some host density below 150 stems per acre, the insect population will be unable to maintain itself. We have no knowledge of the spittlebug damage potential under conditions of very low host density.





# *Matsucoccus resinosae* B. & G. on Red Pine in Connecticut

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## ABSTRACT

This *Matsucoccus* scale was discovered killing plantation red pine, *Pinus resinosa*, in Connecticut in 1946. In 1955, the insect was described as a new species. Since 1946, the insect has spread over 125-150 square miles in Connecticut and New York. Although only several hundred acres of plantation red pine are infested, thousands of acres of reforested land in the Northeastern United States containing valuable watershed plantings and potential timber crops of red pine are threatened. Natural control factors appear to be ineffective in keeping the insect in check. Whether the scale is native or whether it is a foreign introduction has not been determined. For this reason, control efforts have been aimed at obtaining a suitable insecticide spray application which might be used to keep the insect in check. Only one or two chemicals of many tested, when applied in large dosages at high concentrations with ground equipment, have given temporary control of the pest. Survivors rapidly build up, following spraying, to a point where populations are normal one year after treatment.

Red pine, *Pinus resinosa*, and white pine, *Pinus strobus*, are the principal tree species that have been used in reforesting the tens of thousands of acres of farm land abandoned after the turn of the century in the northeastern United States.

One of the more recent pests discovered on red pine is a *Matsucoccus* scale, which was described by Bean and Godwin (1955) as a new species. Thousands of acres of valuable watershed plantings and potential timber crops of red pine are in danger as long as this insect remains active. Trees die about 3 to 5 years after they have become generally infested by the scale.

Since *Matsucoccus* was first discovered in Connecticut in 1946, and subsequently on Long Island, New York, there has been very little change in the distribution of the insect. When the last complete survey was made in 1953, the scale was restricted to approximately 40 square miles on Long Island, scattered spot infestations in Westchester County, New York and another 60 square miles in Connecticut.

In 1955, this area was partially re-examined. The results of the survey show only a continued similarity in the distribution pattern that we have found in recent years. That is, the pest appears to infest new territory at the rate of about 1 mile each year. To be sure, there has been considerable tree mortality, and the insect currently infests valuable watershed plantings, which may eventually succumb; however, spread in terms of great distances or infestation throughout thousands of acres of red pine has not occurred. In both states the actual area infested probably does not exceed 2,000 acres.

Several factors have aided in preventing more widespread dispersion. First, the insect is not well adapted to moving considerable distances under its own power. The wingless females and the tiny mobile crawlers are poor travelers and cannot survive unless they reach suitable host plants within a brief time. Second, red pine is rather sparsely scattered throughout much of the infested area — sparsely in terms of numbers of areas and also in the size of these individual areas. Small isolated groups of infested trees found in many localities may be ineffective focal points for spread of the pest to new centers.

The possibility exists that the insect might be accidentally spread through the movement of ornamental planting stock. The largest home-building program of all time has flourished throughout the *Matsucoccus* zone, and the use of ornamental plants accompanying this boom is phenomenal. Several years ago, this situation was checked in both states involved; however, a periodical review of the problem will be required. Extreme caution will have to be exercised to avert undesirable spread of the scale. Because of this potential threat, surveys will be continued.

Up to 1955, *Matsucoccus* was thought to be host specific. Laboratory and field experiments conducted prior to this time in an effort to establish the scale on other

species of pines were unsuccessful. Twenty-five species of native and introduced pines were used in these tests. Two of the species that were artificially infested in 1954, and again in 1955, now support a normal population of *Matsucoccus* on some branches. These species are Japanese red pine (*Pinus densiflora*) and Chinese pine (*Pinus tabulaeformis*). Initially, these host studies were started in the hope that they might shed further light on the origin of the scale. As yet, the question of whether the pest is native or introduced has not been resolved.

Japanese red pine, one of the two new species infested, is a very popular ornamental plant in wide use at the present time. In the areas in question this pine has replaced red pine as one of the favorite ornamental plants, because of the severe damage done to red pine by the European pine shoot moth, *Rhyacionia buoliana*.

Little can be said about the new host-insect relationship until additional field testing is completed, for we are not certain yet that the insect will infest these trees under natural conditions. This aspect of the problem will be investigated because certainly the potential is tremendous if we consider the movement of ornamental stock as a primary factor in dispersion of the pest.

Now for a few minutes, I would like to turn to the control of *Matsucoccus*. First let us consider the insecticidal testing, which has been going on since 1951. To date about 30 various compounds have been screened and applied in laboratory or field trials. These insecticides encompass almost the entire field of pest control as we know it, since the chemicals include the standard hydrocarbon and phosphorus compounds, fumigants, systemic poisons, miticides, and oil contact insecticides.

It did not take long to realize after preliminary screening had begun that control of this pest would be a difficult task. Perhaps a simple illustration in terms of insect abundance will describe the problem. The following figures are actually taken from 1955 field trials and represent the best results attained thus far. Prior to any control, pre-spray sampling disclosed 100 insects per square inch of bark. After two applications of Chlorthion about 1 week apart we are able to reduce the population by 99 per cent — or to one insect on the initial sample unit. One month after treatment and the start of a new generation the single insect has multiplied to ten, and by the end of summer, following a second generation, we are back to the original 100 specimens per square inch of bark.

The logical question to follow might be: "Why not another application at the right time to kill that 1 per cent?" Frankly, it does not seem possible to do much more than this under plantation conditions unless we wish to consider red pine more as an apple tree than as a reforestation tool or forest crop. When you realize that the most effective chemical, Chlorthion, is currently being applied by mist blower in high concentrations at the rate of 100 to 200 gallons per acre in order to attain 99 per cent control, and that 99 per cent control is only a temporary thing, then I think you begin to visualize the magnitude of further refinements that are required.

As a result of this past season's work, we feel that chemical treatments made in the fall may be more effective than spray applications made in the spring. Although the overall reduction in population is identical at either time of the year, there is a good reason to believe that natural winter mortality may help substantially in reducing the numbers of survivors. This was strikingly demonstrated two seasons ago when a prolonged cold spell with temperatures in the minus 15° to 20°F. range killed a large proportion of the overwintering scales.

Since that initial experience demonstrated that cold might be a limiting factor in either the buildup of the pest or its dispersion into a colder climate, additional testing has continued. This work has been confined primarily to cold-chamber studies. To summarize these cold-hardiness investigations briefly, we can say that adverse temperatures may be an important control periodically. However, even at a temperature as low as minus 29°F., there have always been survivors. Therefore, it is readily discernible that severe winter temperatures may prevent a buildup of populations to damaging proportions in many areas of the northeastern United States; but it in no way indicates that the insect will not survive in these areas.

Other forms of natural control exist, but have not proved to be effective thus far in limiting *Matsucoccus* populations. The pest seems almost impossible to eliminate

event with the tremendous dosages of insecticides that we have been using. So it seems time to consider how best to live with the insect and keep it under control. With this approach we need to learn, among other things, as much as possible about the natural factors that may help us keep the insect at a low level.

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### DISCUSSION

J. J. FETTES. Since this insect is now confined in area and so potentially dangerous to red pine, would it not be worth while to attempt complete eradication regardless of effort?

R. C. BROWN. It would be desirable to attempt complete eradication and we may try to do this when and if an effective chemical control method is found.

W. L. SIPPELL. What native biological agents are active in the infestations of *Matsucoccus* scale in Connecticut? Do any show promise of being effective?

R. C. BROWN. There are a number of effective predators in Connecticut, particularly mites and hemerobiids. They have been observed in check plots but we have little quantitative data because we have concentrated on chemical control.



# Low Winter Temperatures and the European Pine Shoot Moth

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## ABSTRACT

Studies have been made of the effects of low temperatures on mortality, due to freezing, of overwintering larvae of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.). It has been shown that larvae possess a greater ability to undercool than was previously suspected. Overwintering larvae collected from four different temperature zones in Ontario, and two in Michigan, showed no significant differences in their ability to undercool. However, these insects exhibited active cold hardening when held at temperatures between  $+7.0$  and  $-7.0^{\circ}\text{F}$ . for one week prior to the undercooling tests. The insulating effects of snow cover on habitat temperatures have been demonstrated, and from this, it has been postulated that overwintering larvae of the European pine shoot moth, in buds under 8 inches of snow, could survive winter temperatures as low as  $-25^{\circ}\text{F}$ . for an indefinitely long period of time. Potentially dangerous areas for the northward spread of the shoot moth beyond the  $-20^{\circ}\text{F}$ . minimum winter isotherm in Ontario, have been described as those areas that receive a total annual snowfall in excess of 80 inches.





# Studies on the Physiology of the Ambrosia Beetle *Trypodendron* in Relation to its Ecology<sup>1</sup>

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## ABSTRACT

A report is given of investigations carried out as part of a program to determine the role of physiological factors, acting as internal stimuli, on the behaviour of this insect. Laboratory flight capacity studies with mounted beetles showed that continuous flights of several hours are possible and indicate a difference in capacity, or inclination to fly, between beetles seeking logs and those flying to overwintering sites. Response to a flight stimulus during adult life is closely related to condition of indirect flight muscles, which go through a marked but temporary change during the brood-establishment period. Several hundred beetles were dissected to study changes in digestive, reproductive, and other organs during adult life. In the female, reproductive organs, oenocyte colour and extent of head setal wear were used to distinguish between young and old individuals. The high proportion of old adults found in samples of overwintered populations suggests that many females carry out more than one attack-overwintering cycle. It is considered that an adult diapause occurs in this species.

## INTRODUCTION

This paper presents recent findings of a biological and physiological study of the ambrosia beetle, *Trypodendron lineatum* (Oliv.), and briefly discusses these findings in relation to its ecology. The investigations aim to further our knowledge of physiological processes as they affect behaviour. The basic question which orients the work is this: How do factors within the insect influence its responses to external environmental stimuli?

The general pattern of scolytid biology has been well outlined by numerous studies carried out in the past, particularly in Germany (*vide* Escherich, 1923). Hadorn (1933) reviewed the existing information on this ambrosia beetle and added much based on his own work.

*Trypodendron* adults fly only when they are seeking or leaving logs. These flights are important events in their lives, however, and for this reason the study of flight capacity and behaviour received much attention. Another major phase of study involved observations of the appearance of internal organs during the relatively long adult life. This approach was considered basic to more critical studies of internal conditions as related to behaviour.

## FLIGHT STUDIES

Flight capacity was first investigated using balsa-wood flight mills based on Hocking's design (1953). Later it was concluded that flight capacity and behaviour were similar with fixed mounts and these have been used primarily, because they require less time and space. Over 450 beetles, mostly females, have been mounted, placed at room temperature under a desk lamp and observed at frequent intervals for several hours at a time.

The following statements represent generalizations based upon the flight capacity tests. Changes in body position or light intensity appear to have little effect on flying beetles. Individuals caught in flight or removed from forest litter (duff) before spring often fly continuously from one to several hours. Those which have left logs after brood development usually fly for much shorter periods. Performance does not appear to be correlated with adult age (see later section) in either group and the only apparent difference between the sexes is that the longest fliers seem to be females more frequently than males. Considerable variability in flight capacity has occurred in all groups so far tested and each has contained some individuals which, during the test interval, have

<sup>1</sup>Contribution No. 365, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

repeatedly started to fly only to stop almost immediately. Table I presents typical results of flight capacity tests representing two stages of adult life.

TABLE I — Duration of Flight in Groups of 50 Females.

Source of beetles		Time (Hrs.) of longest essentially continuous flight during test										
		Less than						More than				
		1/4	1/2	1	1	2	3	4	5	6	7	8
From litter— early spring	A*	6	8	12	34	20	16	13	10	4	4	1
	B	15	17	23	27	22	14	8	6	4	3	
Emerged from brood logs	A**	35	44	45	2	1						
	B	35	44	45	5	3	1					

\*4 beetles detached from mounts during test.  
\*\*3 beetles detached from mounts during test.

Responsiveness to flight stimulation at different stages of adult life has been determined by tossing beetles into the air, at room temperature. This is best done near a window so that beetles which fly can be retrieved easily. If the beetles fly at any of three consecutive tosses they are considered flight positive, otherwise they are classed as flight negative. In the latter category are beetles which do not react at all, those in which elytra open but membranous wings are inactive, and those in which these wings beat but not sufficiently to sustain the body weight.

Generalizations will again be made, on the basis of tests involving several hundred beetles. Individuals taken from litter in the spring, or while flying, spread their wings and fly immediately when tossed. Those removed from early stages of gallery excavation also fly but later in the brood-establishment period they become flight negative. At least in the early stages of this flight negative condition, however, they become flight positive within a few days if removed from their galleries. Likewise, parent or young beetles dug from galleries before they are ready to emerge are flight negative but respond positively within a few days. In each group in which a change in response is occurring some individuals may be found which flutter their wings but cannot actually fly (the third of the categories of flight negative beetles mentioned in the above paragraph). Table II presents results of typical flight tossing tests with beetles from litter or removed from galleries.

TABLE II — Typical Results of Flight Response Tests.

Source of beetles	Number responding positively	Number responding negatively	Number alive at test date	Per cent flight positive beetles
From litter in spring	94	4	98	96
From log, early brood establishment period* (kept outside galleries).				
June 21	1	61	62	1.6
June 26	23	34	57	40
July 3	50	2	52	96

\*All galleries had eggs and approximately 3/4 had some larvae.

CHANGES IN INTERNAL ORGANS DURING ADULT LIFE

Like other scolytids, *Trypodendron* goes through a sequence of different activities in carrying out its attack cycle. Also, a given individual may carry out one or more re-attacks after completing the first gallery system. Thus samples frequently consist of both young beetles, which have not carried out an attack, and old ones which have completed one or more attacks. Several hundred freshly killed beetles, mostly females, were dissected in order to determine the condition of digestive, reproductive and other organs at different stages of adult life. Some phases of adult history are not yet well

represented in the series studied but certain important internal organ changes have been established.

The ventriculus and often the oesophagus of beetles taken in flight are distended by a large gas bubble. The pumping of air into the tracheal system of other beetles before flight is mentioned by Rüschkamp (1927) and the ventricular gas, probably air, would appear to have some function associated with flight. Individuals without gas in the ventriculus may fly when tossed, however.

The two typically scolytid feeding periods, as young adults just after eclosion, and again during brood-establishment, result in filling of the intestinal tract with fungus particles and fluid. The mid-gut particularly becomes markedly distended, and its cells much thickened. After feeding has ceased the intestinal tract becomes essentially empty, enters a resting phase and appears as it did before log attack.

The fat body, Malpighian tubes, and male reproductive system undergo definite changes in appearance, associated with the sexual activity and metabolic depletion which occur during attack and brood-establishment. These changes are reversible, however, with the building up of metabolic reserves which follows the parent adult feeding period (the "Regenerationsfrass").

The female reproductive system also shows much change, due to egg-laying activity within the galleries, and after brood-establishment returns to a condition essentially similar to that of the pre-attack period. Certain anatomical features, however, indicate that mating and egg-laying have taken place and make it possible to differentiate between young and old individuals. These features include presence of sperm in seminal receptacle and associated "gland", the corpora lutea, and remains of secretion within the colleterial glands (Kittdrüsen). They have been well studied in curculionids or other scolytids (e.g., Nüsslin, 1897; Knoche, 1904; Schwerdtfeger, 1929; Francke-Grosmann, 1951) and used for a long time as a basis for age analysis of adult populations, a key to understanding life history in these groups. It might be mentioned that in *Trypodendron*, the amount of setal wear on the frons of the female, which constructs most or all of the gallery, gives a less precise indication of age without dissection.

Another internal age criterion has been found and promises to be of value, as well as raising the question of its significance. The oenocytes of females taken from litter in either spring or autumn and judged by other criteria to be old, are conspicuous due to their yellow colour, which contrasts with the white fat body in which they are embedded. In young adults, however, the oenocytes are essentially colourless. A similar contrast between oenocytes of males from a mixed population exists. Because males show less head setal wear and their reproductive organ changes appear to be completely reversible it appears that oenocytes will be particularly helpful in determining age in this sex.

The above-mentioned criteria are being used to study certain features of biology in which young and old adults behave differently, as well as to analyse population samples in terms of their age composition (Chapman, 1955). In the study area, surprisingly high proportions of old beetles have been found in litter samples, even in spring. The age composition of such samples is given in Table III. Apparently

TABLE III — Data on Age Composition of Various Samples of Females, Lake Cowichan, B.C. (2,500 ft.).

Sample description	Old adults	Young adults	Number in sample	Per cent old adults
Caught in flight June 1955	36	27	63	57
From litter autumn 1955	31	28	59	52
From litter spring 1956*	133	223	356	37
Caught in flight May 1956	15	11	26	58

\*Sub-samples ranged from 58 per cent of 67 beetles to 6.2 per cent of 32 beetles.



many females survive to attack one or more times after completing the first gallery system but it is not yet possible to determine how many attack cycles an "old" female has completed or to explain the high proportion of old adults in most samples.

An important internal organ change found to occur during adult life is one which explains the period of negative flight response during brood-establishment. After the early stages of gallery excavation the indirect flight muscles become progressively smaller until they become such thin bands of tissue they are likely to escape casual

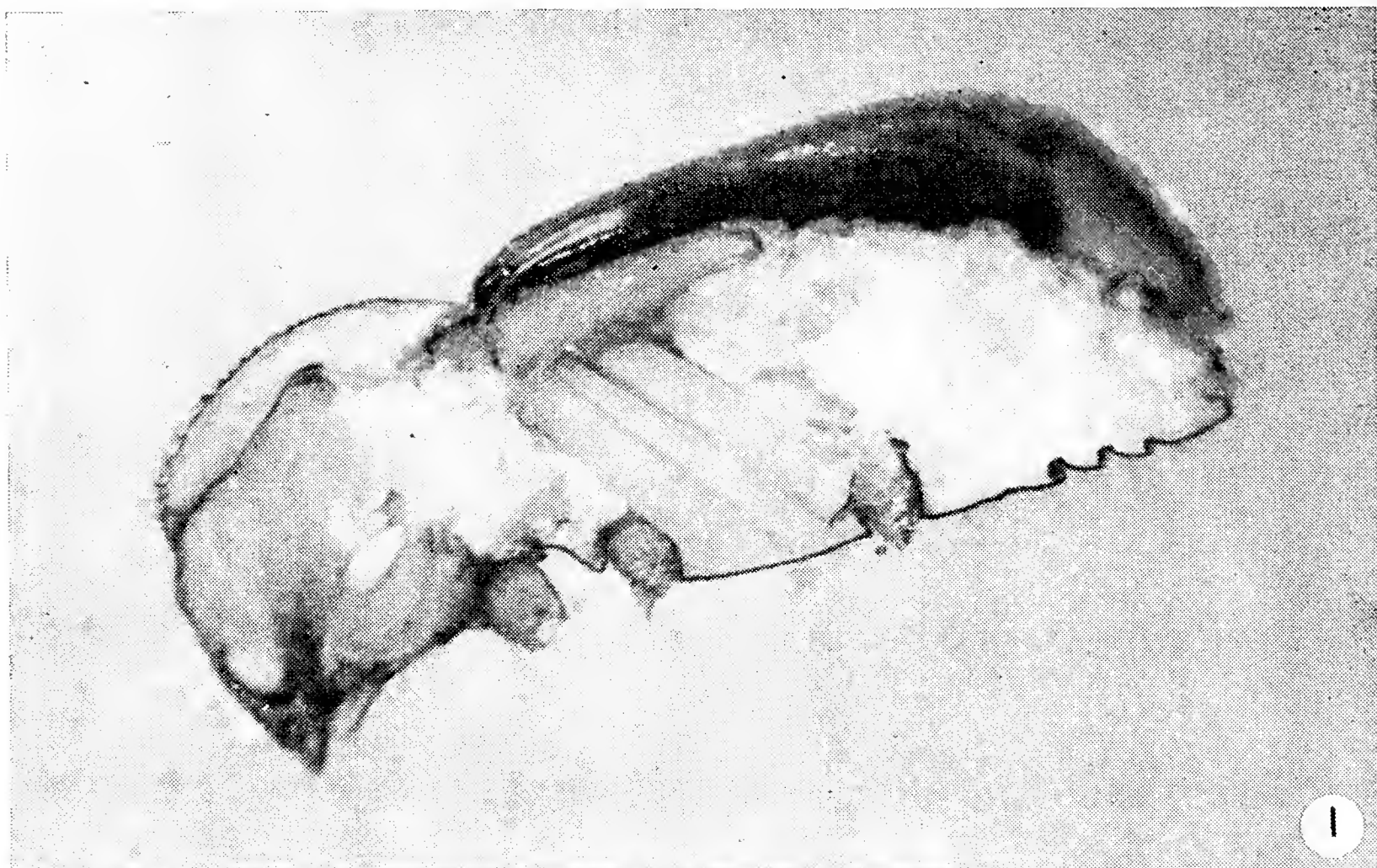


Fig. 1. Half of female taken in flight, preserved and cut along the mid-sagittal plane. Large flight muscles are very conspicuous.

Fig. 2. Half of female taken from gallery and prepared as in Fig. 1. Note greatly reduced flight muscles, with distal portion of elongated ovary (x) adjacent to horizontal muscle remnant.



observation. In beetles which can fly these muscles are a conspicuous feature of internal anatomy and occupy considerable volume in the thorax. When they become reduced in size the space formerly occupied is taken by the ventriculus, then considerably distended with food and, in the female, by the distal portions of the elongated and greatly enlarged ovaries. The reduction in size of flight muscles occurs in both sexes and is only temporary since by the time the parent beetles have finished feeding and are ready to leave the logs these muscles appear to be as large as at the time of initial attack. This flight muscle change is reported and briefly discussed elsewhere (Chapman, 1956). It appears to be an adaptation to a life in which there is need to fly strongly for relatively brief periods but in which most activity occurs within logs. Long confinement within plant tissue, as adults, is characteristic of scolytid life. Nüsslin (1913), for example, stated, "Der typischste Charakterzug der Borkenkäferbiologie ist das fast ausschliessliche Innenleben aller Entwicklungsstadien im Innern der Brutpflanze". An atrophy of flight muscles following the flight period has also been reported for the weevil, *Hylobius*, which remains outside plant tissue as an adult, however (Escherich, l.c.). Figs. 1 and 2 illustrate the flight muscle change in *Trypodendron*.

### GENERAL DISCUSSION

By focusing attention on physiological processes in *Trypodendron* we become better able to study critically its behaviour and to understand its ecology. For, to consider its ecology we must know its life requirements and biological capacities. Under natural conditions material suitable for attack is often widely scattered in forest areas and considerable flight capacity would be expected. The captive flight tests have confirmed that the beetles have ability to fly long distances. As no feeding occurs during flight periods the utilization of fat as fuel is indicated (Weis-Fogh, 1952). The tests also indicate considerable variability between individuals in flight capacity although further studies will be necessary to be sure that experimental artifacts are not involved in results of such tests. The beetles apparently are not so capable of long flights when they leave logs, or their tendency to fly is less then, and there are important ecological implications in either case.

The obligate flightless period within the galleries means that during this time beetles cannot readily abandon logs by flight and that a capacity of primary importance from an ecological standpoint is lost temporarily. The changes in flight muscles are at least partially reversible with time, however. This is indicated by the change in response of individuals to tossing during a period of several days following removal from galleries, either early or late in the brood-establishment period. An explanation thus exists for eventual abandonment by the beetles of galleries which slowly become unsuitable, as with excessive drying of logs. It is puzzling that flight muscle changes occur in males as well as females although the former do little or no burrowing and do not have the additional heavy metabolic demand represented by egg production. The fact that these and other changes involving various internal organs take place together during brood-establishment poses the problem of causal physiological mechanisms. Certainly nutritional and perhaps also hormonal factors are involved.

Clarification of the extent and importance of old adults in the general population at various times becomes possible after study of internal organ changes provides a basis for adult history analysis. Due to re-attacks, dependence of attack and development times upon weather, and other factors, adult populations are often complex in their age composition. Our findings so far substantiate Hadorn's conclusion that young adults, although emerging by mid-summer, do not attack logs that year and that late season attacks, which led earlier investigators to speak of two or even three generations a year, are all re-attacks made by old adults. It appears that young adults enter a condition of diapause after they leave the logs, as implied by Hadorn and as suggested by Schvester (1954) for *Anisandrus dispar* F., another ambrosia beetle. Such a physiological condition has many implications so far as biology and behaviour are concerned. It is obvious that age composition of *Trypodendron* populations is also of much ecological significance.

## ACKNOWLEDGMENT

I would like to thank R. R. Lejeune and W. G. Wellington for reading the manuscript and R. Banyard for taking the photographs.

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# A Study of the Biology and Control of Ambrosia Beetles (Scolytoidea) Attacking Timber in West Africa

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## ABSTRACT

*A short outline is given of the work conducted since 1953 by the West African Timber Borer Research Unit. This small unit of the British Colonial Research Service has made a study of the problem of the extensive damage to timber caused by ambrosia beetles in Nigeria and the Gold Coast. A short discussion of the taxonomy of West African Scolytoidea together with the findings of the ecological and biological studies conducted are given. The results of chemical control tests are outlined and the resulting tentative programme for the protection of logs in West Africa is presented.*

## INTRODUCTION

The defect in timber known as pinworm, pinhole, or shothole damage has become a timber insect problem of major economic importance with the recent increased exploitation of a wide range of tropical hardwoods. The damage is caused by a large group of beetles commonly known as ambrosia beetles which are members of the families Scolytidae and Platypodidae. The problem presented by these beetles was outlined and all the available literature on the subject summarized in a paper by Fisher, Thompson and Webb (1953-54). Since that time, the West African Timber Borer Research Unit, a small unit of the British Colonial Research Service, has conducted studies of the biology and control of ambrosia beetles in Nigeria and the Gold Coast. Concurrently, the work on the association of the beetles with the so-termed "ambrosia fungi" has been carried out by a member of the Unit stationed at the Forest Products Research Laboratory in the United Kingdom. The results of the West African studies only, are the subject matter of the short paper presented here.

## TAXONOMIC STUDIES

During the course of the ecological and biological studies mentioned below, a considerable amount of information has been accumulated on the taxonomy of the West African Scolytoidea. To date forty-six species have been determined and of these twenty-seven are Platypodidae and nineteen are Scolytidae. Nine species are new records for the Gold Coast. From the large number of species as yet undetermined, additions to the recent check list of Gold Coast Scolytoidea by Schedl (1954) may be established. Further contributions were made to our present knowledge of the distribution of this family as presented by Dr. Schedl to the Systematics section of this Congress.

Previous collections of Scolytoidea in West Africa have been deficient in the male representatives of several species. These often differ markedly from the females and several male—female relationships have been established by collections from individual galleries. Immature forms have also been collected and studies of the morphology of these and of the adults as it affects the biology of each species are being conducted. Host lists prepared for each species reveal that some ambrosia beetles are specific to one species of timber whereas others are found on virtually every one of the three hundred odd tree species found in West Africa.

## ECOLOGICAL STUDIES

The first experiments conducted by the Unit in West Africa were designed to elucidate the ecological background of the ambrosia beetles and to determine the factors affecting the density of their attack on newly felled logs.

Trees covering a wide range of diameters were felled at regular intervals throughout one complete climatic cycle. Billets from each tree were exposed to attack in the

forest under all combinations of the following sets of conditions; in sun or under shade; with the bark intact or with the bark removed; lying in contact with the ground or raised on skids. Weekly counts of the overall number of ambrosia beetle entrance holes on a density per-square-foot basis were made on all surfaces of each billet for twenty weeks from each respective date of felling. Weather records were kept at the experimental site for the entire period.

Conclusions which emerged from the foregoing experiment can be summarized briefly as follows:

1) There was no apparent correlation between log diameter and the overall density of attack, although preferences for a particular size of host by individual species of ambrosia beetles were determined.

2) Logs from which the bark had been removed suffered an attack by ambrosia beetles which was greater in density than that sustained on logs left with the bark intact. This difference was maintained for twenty weeks from the date of felling but was more marked in the early stages of exposure to attack. Attacks by other groups of wood-boring beetles such as the Cerambycidae which require bark for oviposition must of course also be taken into consideration in any recommendations for log protection.

3) Differences in the density of attack on the upper, side, and lower surfaces of logs existed but there was no consistency in such differences except in the case of the lower surface of billets in contact with the ground where a heavy attack was sustained. The end cross-cut section of logs sustained a very heavy attack but many of the galleries started there were abortive.

4) There was no significant difference in the degree of attack found on logs left in the sun from that found on those placed in the shade.

5) Logs left on the ground sustained a significantly greater degree of attack than logs raised on skids.

6) The overall density of attack by ambrosia beetles on the logs averaged 72 holes per square foot at each count throughout the entire year. Fluctuations above and below this average were not great and showed no direct or delayed correlations with temperature, relative humidity, rainfall or sunlight hours.

In order that the density of attack would be sufficiently great to reveal fluctuations and correlations, the above long-term studies were conducted using timber of only two genera, *Antiaris* and *Albizia*, which were known to be highly susceptible to attack by ambrosia beetles. A short-term experiment was conducted simultaneously to determine an index of the relative susceptibility to attack of twenty different timbers of commercial importance. Counts of the density of attack on numerous billets of each of these twenty species with bark removed and bark intact were made at regular intervals after felling. The average number of entrance holes per square foot determined six weeks after felling varied from a low of 3.2 on *Turraeanthus vignei* to a high of 230.7 on *Antiaris africana*. Despite this large variation, no correlations were found between the density of attack and any of the following features of the timbers:

wood density;

average bark thickness;

moisture content and starch content of the sapwood and heartwood determined at felling and at regular intervals thereafter; or,

botanical groupings of the timbers.

### BIOLOGICAL STUDIES

The majority of the species of ambrosia beetle found in West Africa are crepuscular in habit. In high-forest areas, the more common species of the genera *Doliopygus*, *Platypus* and *Xyleborus* exhibit the habit of appearing in flight only during the hours of dawn and dusk when temperatures of 21 to 25°C, relative humidities of 88 to 96%, and light intensities of less than 200 lux prevail under the forest canopy. Species of the genera *Eccoptypterus* and *Trachyostus* appear only during the mid-day hours



when light intensities exceed 300 lux and temperature and relative humidity values are 27 to 30°C and 70 to 75% respectively. A further variation in time of activity is exhibited by certain species of the genus *Xyleborus* which are nocturnal in habit and positively photo-tropic.

The restriction of flight activity to these well defined periods during the day results in the sudden appearance of a species in very large numbers on newly felled timber. The impression of swarming is thus created but observations have shown that each beetle seeks its host independently.

Ambrosia beetles attack newly-felled timber almost immediately after felling. The males arrive before the females but infestation by both sexes continues at a steady rate. Weekly observations of the density of attack on numerous logs for the twenty weeks subsequent to felling revealed no sudden increase or decrease in the rate of attack.

Studies of the biology of ambrosia beetles during the large part of the life cycle spent in the seclusion of their galleries in timber are difficult to conduct. Data have had to be built up empirically and study is complicated by the great variety of habits exhibited during this stage of the life cycle.

The average length of life cycle from the infestation of the host by the adult beetle to the appearance of the first imago varies from twenty-eight days (*Eccoptopterus sexspinosus*) to over eight weeks (*Trachyostus schaufussi*). The number of offspring also varies from thirty (*Doliopygus conradti*) to over one hundred (*Xyleborus semi-granosus*). The smaller Scolytidae construct their galleries only in the sapwood whereas the galleries of the larger Platypodidae extend well into the heartwood. The pattern of galleries is quite consistent within a species but varies widely between species. Some species commence their borings on the rounded log surface whereas others show a preference for the cross-cut end section of a log.

Until an effective method of rearing the beetles in the laboratory is developed, biological studies will be limited in scope and will not reveal a true picture of the sequence of the life cycles. Findings will be confined to empiric statements such as those outlined above.

### CHEMICAL CONTROL STUDIES

Concurrent with the ecological and biological studies, numerous insecticides trials were conducted by the Unit. Tests of a wide range of insecticides at varying concentrations have revealed that benzene hexachloride when applied at a concentration of not less than 0.5% gamma isomer content was significantly the most effective. However, the problem is to formulate the BHC in a carrying medium which will impart a long residual effect under the conditions of heavy rainfall and strong sunlight prevailing in West Africa. This is essential as logs often remain exposed to attack in the forest for prolonged periods.

When formulated in a mixture using water as the diluent, the BHC has virtually no residual effectiveness. When fuel oil is used as the diluent, protection is afforded to logs for periods up to two months. However, fuel oil has the disadvantage of being an attractant for the beetles, possibly due to some element such as a terpene which is common to both the oil and newly felled timber, and which produces a chemotactic response in the insects. Whatever the cause, logs treated with fuel oil alone consistently sustained an attack that was almost four times as heavy on the average as that on untreated logs. This attractive effect of the fuel oil was more apparent on bark-intact logs than on bark-removed logs. This may be due to the fuel oil breaking down the masking effect of the bark and the subsequent more rapid release of the attractant from the cambial and sapwood layers.

The problem thus resolves itself into securing a mixture of BHC which does not contain fuel oil but which has a long residual effectiveness. In recent tests, a mixture of BHC in a water-soluble paint which becomes somewhat water-resistant on drying has met the above requirements. The mixture can be diluted sufficiently with water to be applied as a spray. In addition to effectiveness as an insecticide it possesses the property of reducing seasoning checks in logs. Further tests of this material are to be made with attempts at incorporating a fungicide to prevent sapstain on the logs.



### A TENTATIVE CONTROL PROGRAMME

From the results of the biological studies and insecticide tests outlined above, it has been possible to propose a tentative programme of control against ambrosia beetles. In summation, the steps which should prove most effective for log protection in West Africa are:

- 1) Rapid extraction of logs from the forest.
- 2) Bark removal immediately after felling.  
This recommendation is based on considerations of overall insect attack and not just attack by ambrosia beetles.
- 3) Elevation on skids if logs are unavoidably retained in the forest for a long period.
- 4) Treatment as soon as possible after bark removal with a spray containing 0.5% gamma isomer benzene hexachloride formulated in a mixture with water-soluble paint.

### CONCLUSION

The future research programme of the West African Timber Borer Research Unit calls for more detailed studies on the biology and taxonomy of individual species of ambrosia beetles, an attempt at elucidating the true nature of the association between the beetles and the fungi, and a detailed study of the nature of the beetle attractant found in logs. In West Africa where there are such large numbers of so many species and where forest entomology is virtually an untouched field, the work must also be expanded to include studies on other groups of wood-destroying insects.

The authors wish to thank Dr. R. C. Fisher of the Forest Products Research Laboratory in the United Kingdom for his helpful advice, given throughout the course of the above studies. Thanks are also due to Dr. Schedl, Austria; Professor Mayné, Belgium; and Mr. Duffy, British Museum, for their kind assistance in the determination of species.

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### DISCUSSION

H. R. JOHNSTON. Did increasing the gamma concentration of BHC increase the period of protection against beetle attack?

W. E. WEBB. No — not after the minimum strength of 0.5% gamma isomer concentration was used. Any further increase in concentration gave no appreciable increase in period of residual effectiveness.

# Some Laboratory Investigations on the Eradication of Wood-Boring Insects by Gamma Radiation

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## ABSTRACT

Following enquiries concerning the possibility of controlling infestations by wood-boring insects, in particular the death-watch beetle, *Xestobium rufovillosum* (Deg.), by gamma radiation, investigations are now in progress at the Forest Products Research Laboratory in co-operation with the Atomic Energy Research Establishment, Harwell, England. Experiments are being undertaken to ascertain the dosages required to: (a) prevent eggs hatching; (b) kill larvae, arrest their development, or cause them to produce sterile beetles; and (c) sterilize beetles.

Experimental work has been concentrated on the powder-post beetle, *Lyctus brunneus* Steph., which is readily bred in the laboratory throughout the year under controlled conditions of temperature and humidity, thus permitting more rapid assessment of dosages than is possible with the other species under investigation — *Xestobium rufovillosum* and the common furniture beetle, *Anobium punctatum* (Deg.), both of which are much less easily handled in the laboratory.

Since after treatment even at 150,000 r *Lyctus* larvae can live up to 5 weeks, it seems that very high dosages would be needed to produce rapid larval mortality. Adults can be sterilized and the development of larvae inhibited at much lower dosages. In view of the finding that mature eggs of *Anobium punctatum* are much more resistant than newly laid eggs, careful studies not only of the susceptibility of the different stages of the life cycle, but also within the stages, are clearly necessary before the use of gamma radiation treatments as a practical and economic means of control can be considered.

## INTRODUCTION

Radio-active materials have been used for many purposes in entomological research but little has been published on their possible use for controlling infestations of wood-boring insects. Hassett and Jenkins (1952) have given data on dosages which are effective against various stored products insects, amongst which they included some observations on *Lyctus planicollis* Lec. In this species egg-laying was inhibited by irradiation at a dosage of 32,200 r but took place at 16,100 r; it was not stated whether such eggs were fertile. These data have formed a useful basis for the present investigation. The possibility of utilizing waste products of nuclear power as wood preservatives has also been considered, using termites as test insects. With strontium 90 it was found the degree of radio activity necessary to ensure rapid mortality and also to prevent re-infestation within 65 years would constitute a grave danger to man and animals (Sandermann and Casten, 1956).

Infestations of wood-boring insects are normally eradicated by applications of an insecticide, fumigation with a poison gas, or by heat sterilization (Fisher, 1949). These methods are, however, not always applicable in buildings nor completely satisfactory in the case of insects working at a considerable depth within large dimension timbers which themselves are often difficult of access: for example, the death-watch beetle, *Xestobium rufovillosum* (Deg.), an important pest in England of hardwood structural timbers in ancient churches and buildings of historical interest. Alternative methods of treatment are accordingly being sought and of these, irradiation by gamma rays was considered worthy of investigation.

The initial approach to the problem has been purely biological by determining the dosages required to prevent eggs from hatching, to kill larvae, arrest their development or cause them to produce sterile adults, and also to sterilize adults. It is considered essential to have such fundamental data before investigating the possibilities of the

use of such treatments in practice; up to now all experiments have been carried out on small laboratory samples only. This paper constitutes a progress report on the work so far undertaken by the Forest Products Research Laboratory in co-operation with the Atomic Energy Research Establishment, Harwell, England, where the treatments were carried out.

### METHODS AND TECHNIQUE

Although treatment by gamma rays might be satisfactory for infestations by *Xestobium*, this species is unsuitable to employ as a test insect in preliminary investigations since it is not handled easily in the laboratory. The powder-post beetle, *Lyctus brunneus* Steph., however, will readily complete its life-cycle under controlled conditions of temperature and humidity in 3-4 months, thus permitting results to be obtained comparatively rapidly and independently of the normal summer emergence. Consequently, experiments can be repeated to ensure that the results are reproducible. *L. brunneus* has therefore been used for the initial determinations of the range of dosages needed and in the light of these data the programme has now been extended to include *Xestobium* and the common furniture beetle, *Anobium punctatum* (Deg.).

Both beetles and wood blocks which had previously been exposed for egg-laying and contained eggs or larvae were irradiated by a cobalt 60 source at dose rates varying between 1200 and 1300 r/min. Some material was also irradiated at 50 r/min.

Wood blocks approximatively 4 by 1 by  $\frac{1}{2}$  inches or smaller were used—the smaller ones for studies of the effect on eggs, the larger for larvae. For egg-laying, small sapwood blocks of oak *Quercus robur* L. were employed for *Lyctus*: for *Anobium*, sapwood blocks from Corsican pine *Pinus nigra* Arnold var. *calabrica* Schneid. with the end grain covered with muslin, were used (Bletchly, 1952), and for *Xestobium*, decayed oak sapwood. For investigations on larvae of *Lyctus* and *Anobium*, sapwood blocks of oak and Corsican pine respectively, estimated to contain very small, approximately half-grown or mature specimens, have been treated so as to obtain information on the effect of irradiation at different stages of development.

Larvae of *Anobium* are being studied by transferring them to blocks before irradiation (Becker, 1942). Beetles of all three species have been irradiated in small glass tubes and subsequently provided with egg-laying blocks for studies of their fertility. The sexes have been irradiated together or separately and then crossed with untreated beetles to study differential susceptibility.

### BIOLOGICAL RESULTS

EGGS: Owing to the time needed to find and examine *Lyctus* eggs, laid as they are within the vessels of the wood, studies have been concentrated on the eggs of *Anobium* and *Xestobium*, which are laid superficially. Eggs of *Anobium* between 1 and 3 days old were sterilized by 2,000 r but when 22-23 days old, even at the highest dosage so far tested (16,000 r), 61% still hatched. No eggs of *Xestobium* up to 10-13 days old hatched after treatment at 4,000 r, whereas when the eggs were 23-26 days old, a dosage between 24,000 r and 32,000 r was required; of the more mature eggs, however, (up to 33 days old) 27% hatched at the highest dosage used (32,000 r).

It is thus seen that the resistance of *Anobium* and *Xestobium* eggs increases with their stage of development. Similar results have been noted in *Drosophila* (Duggar, 1936).

No studies have yet been made on the subsequent development of the larvae arising from the irradiated eggs.

LARVAE: Investigations were first directed towards the possibility of using lethal dosages for treating infested wood. In order to observe survival rates, larvae of *Lyctus* were removed from infested wood and, following exposure to different treatments, kept in the laboratory in small glass dishes containing frass. No quick "knock down" was thus obtained. The survival rate over the range of treatments from 8,000 r to 150,000 r was approximately proportional to the dosage given, the extreme limits being marked by the survival of one larva for 4 weeks after irradiation at 150,000 r as compared with 24 weeks for one out of 23 untreated controls.

In view of these results attention has been turned to possible sub-lethal effects on larvae irradiated within infested wood. In general it seems that the number of *Lyctus* larvae which can develop normally, whether they are small, half or fully grown at the time of exposure, is reduced by irradiation at 4,000 r, but that the beetles which do emerge are fertile. Emergence from blocks irradiated at dosages of 6,000 r is apparently exceptional and only one beetle (a female) emerged after irradiation at this dosage.

So far experiments with *Lyctus* larvae irradiated at 50 r/min. do not show that they are less susceptible at this lower dose rate.

Emergence has occurred from some of the blocks containing *Anobium* larvae exposed to dosages up to and including 6,000 r but not above. The fertility of the emerged beetles is being investigated. *Xestobium* larvae have not yet been studied.

**PUPAE:** The little work so far carried out on this stage has been on *Lyctus*: fertile eggs were laid after both sexes had been irradiated at 4,000 r; there are little data on the effects of higher dosages.

**ADULTS:** Irradiation of adults might affect the period of their life, disturb the egg-laying capacity or induce sterility. No adequate data have been collected on the length of life; observations on *Anobium* indicate that the egg-laying capacity is not affected to any extent up to dosages of 16,000 r. Since there appears to be a marked effect on fertility, studies have been concentrated on this aspect.

Direct irradiation of both sexes of mature *Lyctus* beetles appears to have little effect on fertility at dosages of 2,000 r but it is greatly reduced at 4,000 r. Exceptionally, fertile eggs can be laid after irradiation at higher dosages. From the blocks exposed to beetles for egg-laying after irradiation at 6,000 r only one beetle (a female) emerged, the highest dosage at which any emergence has so far occurred. That emergence at such dosages is exceptional is shown by the following data: 3 males and 4 females irradiated at 6,000 r laid 52 eggs, all infertile, whereas the same number of control beetles laid 78 eggs all fertile. Although nearly all *Lyctus* adults are sterilized at dosages between 4,000 r and 6,000 r, egg-laying is not inhibited, sterile eggs being laid by beetles exposed to much higher dosages — up to at least 48,000 r.

The susceptibility of *Xestobium* adults is comparable. Of 130 eggs laid by beetles irradiated at 4,000 r, 92% failed to hatch and of 150 eggs irradiated at 8,000 r, none hatched. The results with *Anobium* were similar; at 2,000 r, 97% were sterile; at 4,000 r, 98%; and at 8,000 r, 100%.

The question of differential susceptibility of the sexes has been partly investigated but has not proved easy of solution, since in both *Lyctus* and *Anobium* mating often occurs before the beetles can be collected. Further, they have the habit of re-entering exit holes. Furthermore, in *Xestobium* recognisable external sex characters are absent. Female *Lyctus* beetles collected soon after emergence and segregated from the males laid eggs all of which so far as could be ascertained were fertile. The following table shows the results obtained when both sexes of *Lyctus* were irradiated or either males or females only, the irradiated individuals then being mated to untreated beetles of the opposite sex.

Fertility Per Cent of Eggs Laid by *Lyctus brunneus* Steph.  
after Irradiation of:—

Dosage	Both sexes	Males only	Females only
4,000 r	22	83	75
6,000 r	0	94	48
8,000 r	0	84	37
Untreated controls	100%		

Since after both sexes had been irradiated at 4,000 r only 22% of the eggs laid were fertile and none at 6,000 r, it was concluded that the fertility of one or both sexes was affected. On the other hand, when the males only were irradiated and mated



to untreated females, 84% of the eggs were fertile even after a dosage of 8,000 r. When the females were irradiated and mated to untreated males there was a progressive drop in fertility to 37% at 8,000 r. The high fertility found when only the males were irradiated is thought to be due to the eggs having been fertilized through a previous mating of the females. From this result and from the numbers of fertile eggs laid when only females were irradiated at relatively high dosages as compared with the data when both sexes were irradiated together, it is concluded that the fertility of female *Lyctus* beetles is less affected by irradiation than the males. In the screw-worm, *Callitrogra hominivora* (Cqrl.) (Diptera), a higher dosage was also needed to produce sterility in the females (Lindquist, 1955).

So far data concerning the transmission of sterility to subsequent generations of *Lyctus* beetles derived from irradiated parents are inconclusive.

### CONCLUSIONS

It is clear that biological studies must be completed before the practicability, methods, and economics of normal application can be explored. For instance, it is essential to determine the minimum dosage at each stage of an insect's life-cycle which inhibits further development. Studies of the egg have revealed that widely differing results would be obtained by irradiating at different stages of their development. The indications that the females are more resistant than the males and might therefore be able to mate with males which had escaped treatment and so produce fertile eggs, are of significance in determining the effective dosage which would be needed in practical application.

It is of interest to note that the results obtained with the three species studied are similar.

To sum up, the results obtained so far are promising and justify further work. It appears that although the high dosages required to kill the larvae are not likely to be practicable or safe to use for eradicating infestations in buildings, yet prevention of the completion of development of *Anobium* and *Lyctus* larvae and sterilization of the adults of all three species can be achieved at much lower dosages. This is of particular interest in relation to *Xestobium* — in which, unlike the other two species, the adults remain within the timber for a period of some months prior to emergence. In view of the high resistance of mature eggs of *Anobium* and *Xestobium*, the use of gamma rays for their destruction offers little hope of practical application.

### ACKNOWLEDGEMENTS

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## DISCUSSION

R. J. KOWAL. Has any work been done to determine the depth of penetration of gamma rays into wood?

J. D. BLETCHLY. The work I have carried out has been entirely biological and the physical aspects have still to be investigated; these will be carried out by the Atomic Energy Research Establishment, Harwell. Data are, however, available which show that the measure of penetration which can be obtained is promising in relation to possible future application.



# Comparison of Black Pine Leaf Scale Population-Density on Normal Ponderosa Pine and Those Weakened by Other Agents

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## ABSTRACT

A study of an infestation of black pine leaf scale, *Nuculaspis californica* (Coleman), on ponderosa pine revealed a direct correlation between the degree of damage to the tree and the population-density of the scale insects. This correlation can be explained by assuming that either (1) the scale insects cause the damage, or (2) the scale insects attack more readily trees damaged and weakened from other causes. Tests of the latter hypothesis produced the following results. (1) No significant difference in average population density of black pine leaf scale was noted between trees damaged by infestations of dwarf mistletoe and trees not so damaged. (2) Significantly lower average scale population-density was noted on trees damaged by boron compounds used as weed killers than on trees not so damaged. (3) No significant difference in average population-density was noted between trees with moderate needle tip dieback presumably caused by uptake of atmospheric fluorides and trees not showing such damage. (4) No significant difference was found in average scale population-density between those trees with relatively high fluoride content and those with relatively low fluoride content.

It is concluded that damaged and presumably weakened trees are not more susceptible to attack by black pine leaf scale than are trees not so damaged or weakened. The factors responsible for the scale outbreak are assumed to be principally extrinsic, and additional studies have further supported this view.

This study presents one phase of an investigation of an outbreak of black pine leaf scale, *Nuculaspis californica* (Coleman), on ponderosa pine in Spokane County, Washington in the summers of 1954 and 1955. The principal purpose was to investigate the effect of weakening of ponderosa pine by other agents on the populations of black pine leaf scale.

The populations of scale on each tree were determined by a visual impression method. By comparing the scale population on the accessible limbs of each tree with a graded series of color photographs of known scale insect populations, it was possible to make a sufficiently accurate estimate of the scale population-density on each tree for comparative purposes.

It was apparent from general observations that the degree of damage to ponderosa pine was directly related to the scale insect population-density. To check this apparent correlation, over 1000 trees were examined for scale population-density and condition. This study revealed little difference in condition between uninfested trees and those with scale populations up to about one scale per inch of needle, but greater scale populations are directly correlated with increased damage to the tree in the form of shortened needles, poor needle retention, and probably reduced growth.

This correlation can be explained by assuming either of two hypotheses, namely that (1) the scale insects have caused the damage, or that (2) the scale insects attack more readily trees damaged and weakened from other causes. The latter hypothesis was tested by determining the scale insect population-density on sets of trees weakened by various agents and comparing them with the scale population-density on sets of trees not so weakened that were of the same height and growing under similar conditions.

Dwarf mistletoe (*Arceuthobium*) is one of the most important agents responsible for weakening and death of ponderosa pine. From areas where dwarf mistletoe and black pine leaf scale occurred together, we observed and recorded the scale population of 50 trees weakened by infestations of dwarf mistletoe and 50 trees of comparable size and growing site that had no visible dwarf mistletoe infestations. The average scale population-density of the trees without mistletoe was slightly higher, but the difference was insignificant. Similar differences would be expected to occur by chance alone eight or nine times in ten such similar samples.

Chemical weed killing agents (Borascue) containing boron are used to control weeds along the edges of highways in the Spokane area. These weed-killing agents cause needle-tip dieback on ponderosa pine and may kill such trees. From an area where weed-killer damage and black pine leaf scale occurred together, we observed and recorded the scale population of 50 ponderosa pine trees weakened by boron compounds and 50 trees of similar size and growing site not so damaged. The undamaged trees averaged nearly twice as many scale insects per inch of needle as the boron damaged trees. The difference is highly significant. It is possible that boron compounds are not only toxic to the pines, but to the scales as well.

Atmospheric fluorides when absorbed by ponderosa pine in sufficient concentrations are known to produce needle tip dieback. From an area where trees presumably damaged by uptake of atmospheric fluorides and black pine leaf scale infestations occurred together, we observed and recorded the scale population-density on 50 pines that had moderate needle tip dieback and on 50 pines of comparable size and growing site without such damage. The pine trees without needle tip dieback had a slightly greater average scale population-density than did trees without such dieback. This difference was not significant, being of a degree that would be expected to occur by chance alone in one or two times in ten such similar samples.

Because of the possibility that fluorides *per se* rather than the injury caused by fluorides might in some way influence scale populations, samples from each of the one-hundred trees used in the last observations were analysed for fluoride content. After eliminating four samples that were invalid for various reasons, the scale populations of the 48 trees with the highest fluoride were compared with the 48 trees with the lowest fluoride content. The trees with the higher fluoride content had an insignificantly greater scale population-density, being of a degree that it would be expected to occur by chance alone in one out of ten such similar samples. Lest it be inferred that this difference *might* be significant, an additional evidence that it is a sampling variation is seen in the fact that the ten trees with the highest fluoride content had lower average scale population-density than did the ten with the lowest fluoride readings.

From our observations we have concluded that ponderosa pine trees that have been weakened by other agents do not serve as hosts for greater populations of scale insects than do normal trees. The idea that weakened trees are more readily attacked by black pine leaf scale has been transferred by inference from evidence that weakened trees are particularly susceptible to attack by pine bark beetles (*Dendroctonus*) and other bark beetles. The "weakened tree" concept is probably applicable only in those cases where (1) there is a weakening of some active defense mechanism which the tree employs against an attacking insect, (2) the weakened tree affords changed ecological conditions that favor the attacking insect, or (3) where the weakened tree presents changed ecological conditions detrimental to predators or parasites of the attacking insects.

In the investigated outbreak of black pine leaf scale the factors responsible for the outbreak appear to be extrinsic. Additional studies have further supported this view.

# Etude biologique, éthologique et écologique de *Platyscapulus auricomus* Schauf. (Scolytoidea: Platypodidae)

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## RESUME

*L'aspect et la variation des attaques d'un Platypode mycétophage sur des bois en grumes est expliquée par sa biologie, son éthologie et son écologie.*

*Parmi les nombreux Scolytoidea mycétophages des forêts de basse Côte d'Ivoire, le Platypodidae Platyscapulus auricomus Schauf., qui fait l'objet de cette note, n'est pas l'un des plus importants du point de vue économique; mais il présente l'avantage d'être monophage ce qui nous a permis d'étudier plus aisément sa biologie, l'éthologie, de ses attaques électives sur les essences du genre Macrolobium et l'influence des facteurs externes sur sa répartition saisonnière.*

*Ajoutons que ces attaques se concentrent sur les échantillons frais non écorcés, à l'exclusion de celles de tout autre Scolytoidea, tant que le bois reste frais; d'autre part, plusieurs Xyleborus s'attaquent aux échantillons non écorcés, frais ou non.<sup>1</sup>*

## BIOLOGIE DE PLATYSCAPULUS AURICOMUS

Les mâles adultes s'attaquent aux échantillons frais dès leur dépôt en forêt et creusent un couloir d'attente. Les femelles surviennent ensuite et recherchent les mâles; après accouplement, le couple disparaît dans les bois. L'espèce est monogame. La population des bois attaqués est composée de 53 à 77 femelles pour 100 mâles; c'est le nombre des femelles qui détermine l'intensité des dégâts.

Le nombre total d'attaques dénombrées sur un échantillon croît jusqu'au 15<sup>e</sup> jour d'exposition. Il peut atteindre, au mois de septembre (l'un des mois les plus favorables aux insectes), plus de 4 attaques par dm<sup>2</sup>.

C'est la femelle qui creuse la galerie, refoulant derrière elle les fibres de bois arrachées. Le mâle, qui la suit, les comprime alors en un bouchon refoulé hors de la galerie. La femelle creuse 5 à 8 mm. par jour et dépose ses oeufs dans la galerie maternelle. Les larves nouvellement écloses passent au-dessous de la mère et, dès lors, celle-ci cesse tout travail dans cette galerie; mais elle en creuse une autre, en dérivation. Le nombre de dérivations dépend de la longévité des insectes (une femelle peut vivre plusieurs mois), laquelle dépend elle-même du maintien des conditions favorables dans le bois.

Le rôle de la femelle et celui du mâle sont nettement définis: la femelle creuse et pond; si le mâle est prélevé de la galerie, elle refoule, avec les fibres, tout ce qui est derrière elle, y compris ses oeufs, et le rejette hors du bois. Le mâle a un rôle plus complexe; il arrête le mouvement de recul de la femelle, ne fait passer derrière lui que les fibres de bois, respectant les oeufs et de multiples débris. Le bouchon qu'il refoule nettoie par frottement les parois de la galerie et assure son herméticité. Le champignon *Ambrosia*, associé au Platypode, ne commence à se développer que dans l'espace non frotté compris entre la femelle et le mâle. Lorsque les larves éclosent et que la femelle leur abandonne le fond de la galerie, le champignon y étend son mycelium.

La femelle commence à pondre 2 ou 3 jours après l'accouplement; elle pond 10 à 20 oeufs non agglomérés que le mâle pousse vers l'avant avec la tête au fur et à mesure que s'approfondit la galerie. L'incubation dure environ 10 jours; la croissance des larves 17 à 20 jours; la nymphose 6 à 10 jours. Les adultes nouvellement éclos s'envolent 36 à 40 jours après la formation du couple fondateur.

<sup>1</sup>Cette note est extraite d'un important travail de P. Cachan: "Les Scolytoidea mycétophages des forêts de basse Côte d'Ivoire. — Problèmes biologiques, éthologiques et écologiques." (Thèse Sciences Paris 1956; parue dans la Rev. Path. Veg. et Entom. Agric. 36 (1-2). Paris. 1957).



Les larves ne creusent pas de galerie; le seul travail qu'elles semblent effectuer est le forage de leur loge nymphale disposée perpendiculairement à la galerie. Leur contenu intestinal et la composition de leurs excréments montrent que leur nourriture est à base du mycelium du champignon et de quelques éléments assimilables du bois; fibres et spores ne sont pas digérées. Les adultes, après leur envol, transportent les spores d'*Ambrosia* ainsi que des spores étrangères appartenant aux genres *Fusarium*, *Penicillium*, *Aspergillus* et *Diplodia*. La protection et le nettoyage purement mécanique de la galerie par le mâle quand il refoule le bouchon de fibre derrière lui s'oppose à la pénétration d'éléments étrangers quand la famille est fondée; mais la prédominance du champignon *Ambrosia* dans la galerie à l'endroit où se développent les larves est le résultat d'une compétition, l'*Ambrosia* étant mieux adapté aux conditions particu-

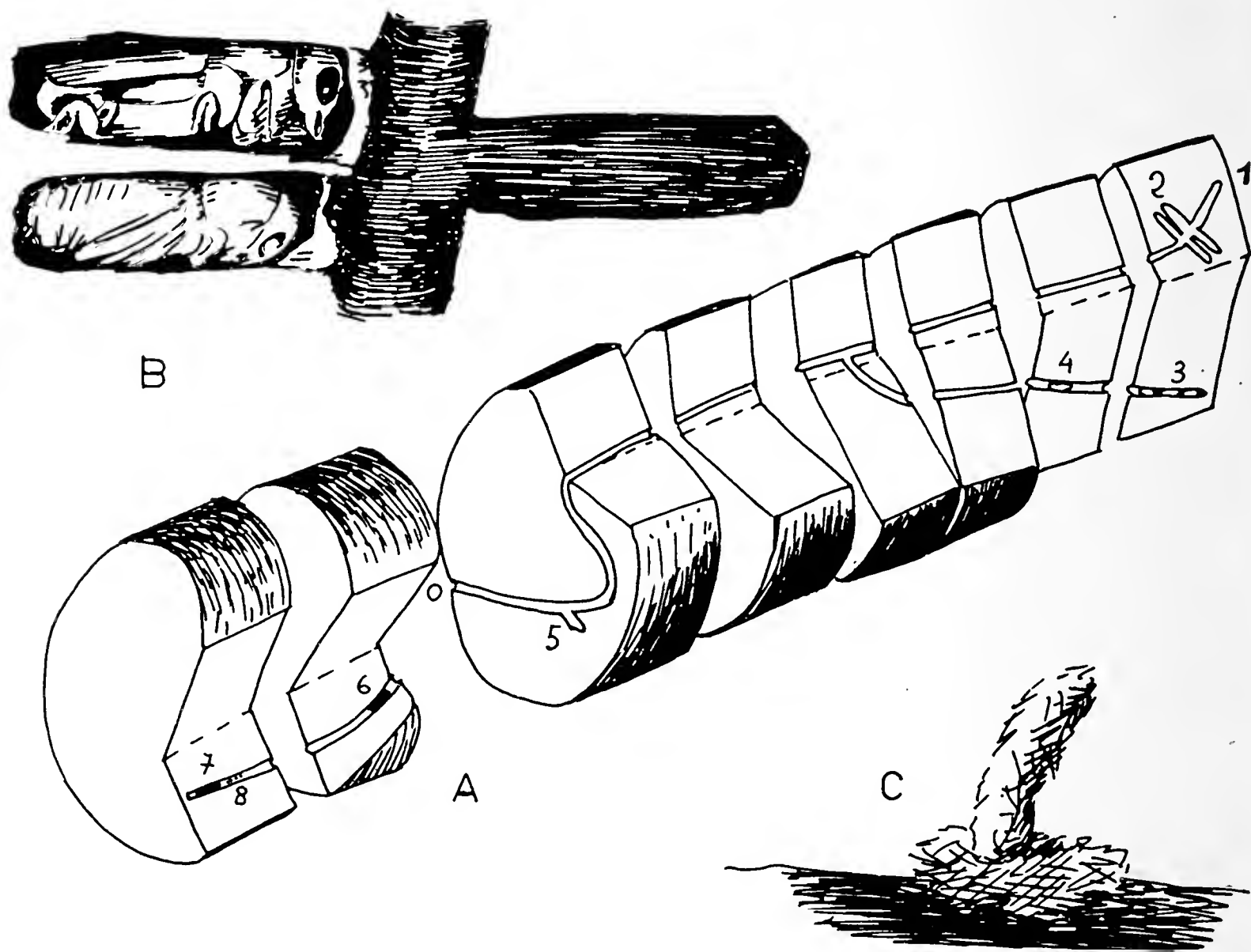


Fig. 1. Biologie de *Platyscapulus auricomus* Schauf.

A. Plan schématique d'une galerie depuis l'accouplement jusqu'à la sortie des adultes nouveaux. o: orifice d'entrée de la galerie; 1: extrémité de la première galerie; 2: loges nymphales; 3: première dérivation; 4: larve avant la nymphose; 5: deuxième dérivation; 6: mâle; 7: femelle creusant; 8: oeufs.

B. Une nymphe et un adulte immature dans leur loge nymphale: noter l'opercule qui les sépare de la galerie principale et la disposition relative des loges.

C. Aspect d'un tortillon de fibre refoulée par le mâle; le cône de débris fait au début du forage est encore visible.

lières du milieu et plus résistant au broutement continu. Les prélèvements faits dans les galeries, trois, neuf et vingt jours après le début du forage, etensemencés sur milieu de culture, montrent que l'abondance du champignon *Ambrosia* va croissant, alors que celle des champignons étrangers va diminuant.

Le champignon *Ambrosia* associé à *Pl. auricomus* lui est vraiment spécifique; en effet, dans les galeries des *Xyleborus alluaudi* et *semigranosus* qui s'attaquent aux échantillons écorcés de *Macrolobium*, les champignons présents ont des spores dont taille, forme et mode de germination sont différents. A l'association champignon-insecte, on doit ajouter un Nématode saprophyte qui semble être spécifique.

CAUSES ÉTHOLOGIQUES DE LA SPÉCIFICITÉ DES ATTAQUES: Dans la nature, on observe que des échantillons écorcés ou de l'écorce isolée de *Macrolobium* ne sont pas attaqués; que des échantillons dont l'écorce a été décollée mais non enlevée, le sont beaucoup moins que des échantillons non écorcés. Mais, si dans ces derniers, on creuse des trous de 2 mm. de diamètre, les attaques s'y concentrent. Des études expérimentales à l'aide d'un olfactomètre adapté au comportement particulier des Platypodidae ont permis d'analyser les facteurs attractifs du *Macrolobium* à l'égard du *Platyscapulus auricomus*.

L'attractivité absolue de chaque partie des échantillons: écorce (E), bois (B) et bois avec écorce (BE), a d'abord été étudiée.

D'autre part, les différents éléments ont été comparés deux à deux. L'étude des couples BE et E, B et BE, montre que les insectes se dirigent vers l'élément où B est

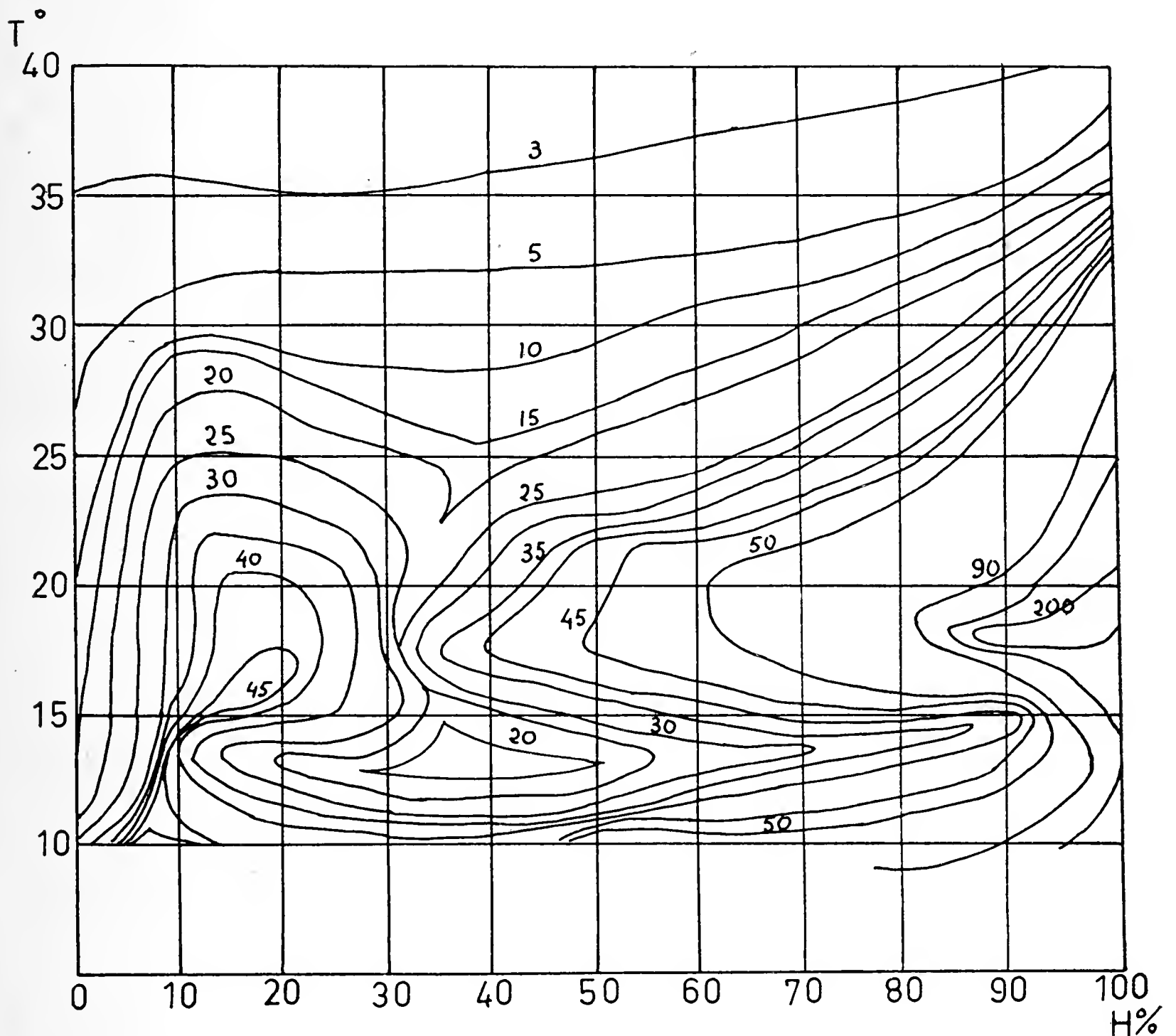
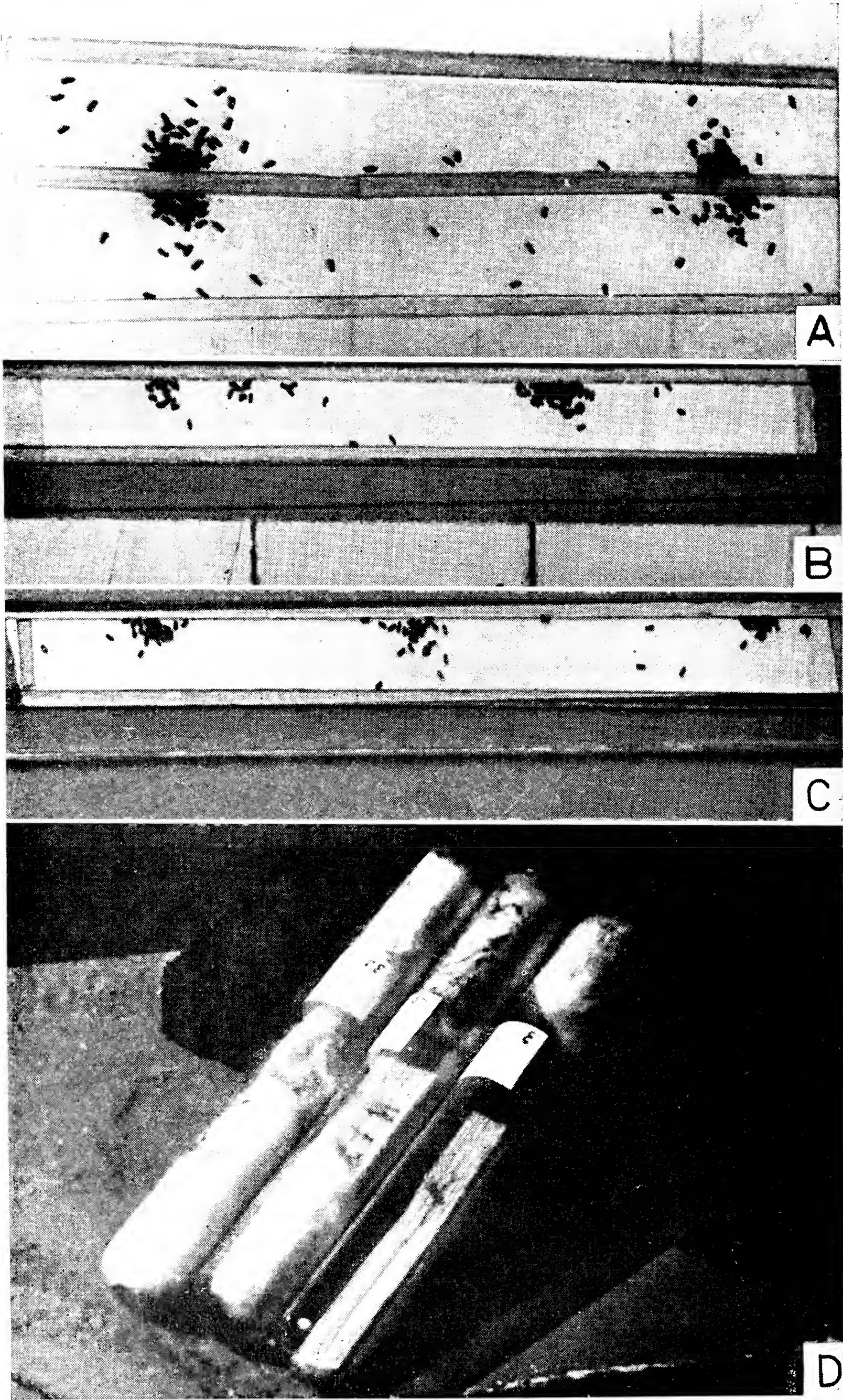


Fig. 2. Ecologie de *Platyscapulus auricomus* Schauf. Diagramme de survie des adultes en fonction de la température et de l'humidité ambiantes. Les lignes relient les points correspondant à une même longévité moyenne comptée en heures.

présent; dans le premier cas, ils vont vers BE et non vers E ce qui correspond à une phase fixation. Dans le deuxième cas, les insectes vont vers B et non vers BE, ce qui correspond à une phase pénétration. Les femelles sont plus nettement attirées que les mâles.

L'étude du couple E et B soulève un problème plus complexe. A la bifurcation de l'olfactomètre, ils ne vont pas vers B comme on pourrait s'y attendre, mais vers E; c'est que le mélange des odeurs venant de B et de E n'agit pas comme celles provenant du complexe BE. Ceci explique le fait, mentionné ci-dessus, que les échantillons dont





l'écorce a été décollée sont très peu attractifs; et, pourtant, les deux éléments sont présents.

En résumé, les attaques semblent résulter d'une succession de comportements dirigés par des stimuli spécifiques:

1. — attraction des mâles et des femelles par le bois et, surtout, par l'écorce;
2. — fixation des mâles dans l'écorce, mais seulement si le bois est étroitement sous-jacent;
3. — pénétration des femelles dans le bois qui est alors, et seulement à ce moment, le facteur stimulant essentiel, plus attractif que le complexe bois + écorce.

Les extraits d'écorce et de bois solubles dans divers solvants comme l'éther, l'alcool et l'eau, sont attractifs à des degrés très divers; mais l'extrait éthéré d'écorce et l'extrait alcoolique de bois le sont particulièrement; ce dernier attire fortement les femelles, ce qui confirme les résultats précédents.

L'attractivité des extraits décroît rapidement. Ceci explique qu'en forêt les attaques cessent après 15 jours d'exposition. Mais il n'en est pas de même pour les autres Scolytidae du genre *Xyleborus* qui s'attaquent aux échantillons frais écorcés et aux échantillons non écorcés lorsqu'ils se sont desséchés. La spécificité des attaques de *Pl. auricomus* sur les échantillons non écorcés de *Macrolobium* semble donc être due à des corps contenus dans l'écorce et dans le bois; mais ceux présents dans l'écorce sont instables et répulsifs pour les Scolytoidea mycétophages autres que *Pl. auricomus*.

Si l'on utilise, comme substrat où peuvent se déplacer les insectes, des chromatogrammes des extraits mentionnés ci-dessus, on observe que ces insectes se groupent en plusieurs points; il y a, sans doute, dans chaque extrait, plusieurs corps attractifs.

**ÉCOLOGIE DES LARVES:** Trois facteurs agissent sur le développement des larves: la température, la teneur en eau du bois et la croissance du champignon *Ambrosia*, laquelle dépend elle-même des deux premiers facteurs. Les larves se développent normalement quand la température est comprise entre 12° et 30°5 et quand l'air des galeries est saturé; mais les exigences du champignon sont plus grandes que celles des larves au point de vue teneur en eau du bois: plus l'humidité est forte au-dessus de 30%, mieux il croît; la croissance des larves dépend donc, en fait, de la température et de la croissance du champignon; le poids des larves est fonction de cette dernière. La vie larvaire passe de 28 jours à 38 jours quand la température décroît de 28° à 15°. D'autre part, plus les larves sont âgées, mieux elles s'accommodent de teneurs faibles.

**ÉCOLOGIE DES ADULTES:** Les adultes se nourrissent peu et résistent très bien à l'inanition. Cette particularité permet d'étudier leur survie en les soumettant à diverses ambiances dont la température est comprise entre 10° et 40° et l'humidité relative entre 0 et 100%. Au-dessus de 35°, les insectes meurent rapidement; ils s'immobilisent au-dessous de 15°, mais peuvent vivre assez longtemps. A 30% d'humidité correspond une longévité minima pour les températures moyennes. Au-dessous de 30% d'humidité,

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← Fig. 3. Ethologie de *Platyscapulus auricomus*. Sur des chromatogrammes d'extrait de bois ou d'écorce, des insectes, placés au hasard entre le substrat et une plaque de verre séparés par un espace de 2 mm. (diamètre d'une galerie), se groupent aux points d'attraction maxima.

A: Chromatogramme de l'extrait alcoolique d'écorce par le mélange n-Butanol (9) et acétone (1).

B: Chromatogramme de l'extrait alcoolique de bois par le mélange n-Butanol (9) et acétone (1).

C: Chromatogramme de l'extrait éthéré d'écorce par l'acétate d'éthyle.

D: Ecologie des larves; la croissance des larves dépend de celle du champignon *Ambrosia*: croissance du champignon *Ambrosia* sur des échantillons de bois à divers degrés de dessèchement à température ambiante; de gauche à droite; bois frais, bois ayant 60% d'eau; bois n'ayant que 30% d'eau.

la longévité peut augmenter jusqu'à 50 heures; cette longévité anormale ne représente, sans doute, qu'une régulation physiologique particulière entraînant une augmentation de la résistance au dessèchement.

Par contre, au-dessus de 30% d'humidité, la longévité s'accroît considérablement lorsque l'humidité augmente; elle peut dépasser 200 heures. Dans cette zone qui correspond aux réactions normales de l'insecte dans des conditions normales, l'écart supportable de températures croît quand l'humidité augmente. Autrement dit, plus l'humidité augmente, plus l'écart des températures supportées est grand. La température optima est 18° dans les hautes hygrométries. Ces résultats de laboratoire permettent d'expliquer la variation saisonnière des attaques de *Pl. auricomus*: les saisons humides et pluvieuses sont les plus favorables à la pullulation de cet insecte, ainsi que les saisons où la température est la moins élevée.



# Forest Entomology in Southern United States

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## ABSTRACT

*Probably greater progress is being made in forestry in the southern part of the United States than anywhere in the world; the country's future capacity to produce timber lies in the South. Forest entomology is rapidly assuming a more important part in this progress.*

*Historically, forest entomology in the United States began in the South; many notable forest entomologists have worked there, including Hopkins, Craighead, Snyder, St. George, Beal, Balch, and Blackman. However, progress in the following years was slow; only two laboratories existed which were intermittently manned by one or two men. Emphasis was on forest products insects research in which notable progress has been made. About 1945 a series of destructive forest insect epidemics began to develop. At the same time forest management was becoming intensive and vast planting programs began. The pales weevil, pine-tip moths, pitch moths, and other insects assumed important status. Land-managing agencies became concerned. Funds for research increased but were insufficient to deal with the many problems. In 1947 the Federal Forest Pest Act was passed and soon forest insect survey personnel were assigned to laboratories at Gulfport, Mississippi, and Asheville, North Carolina.*

*Since then forest insect detection programs have been set up throughout the South in co-operation with forest-managing agencies, and there have been a number of large-scale co-operative insect control programs, particularly against bark beetles. Special effort has been made to inform forest-managing agencies of insect problems and needs for research and control. As a result, the states and industry are adopting forest pest control programs and several states have passed pest control laws. Virginia, North Carolina, and Tennessee have employed pest control specialists and Union Bag and Paper Company and Bowater Southern Paper Corporation have employed forest entomologists. Forest Pest Action committees have been organized in a number of states and new ones are being formed.*

*Emphasis in future program will be placed on improved detection and control through silvicultural and biological methods.*

## INTRODUCTION

Probably nowhere in the world has greater progress been made in forestry during recent years than in the southern United States. Vigorous activity in all fields of forestry indicates that prospects for the future are very promising. As forest resources and values increase, it is inevitable that forest entomology should assume greater importance in forest protection.

The extreme variation in topography, climate, and forest types (Fig. 1) which characterizes the South favors the activities of a vast number of insects, many of them very destructive to the forest. Recognition of the importance of the damage they cause has come slowly. For many years forest fires, which presented a major obstacle to forestry in the South, occupied a foremost position in forest protection. Then too, timber values were low. However, as the value of forest products increased, as forest management became more intensive, and a vast complex of forest industries developed, the need for protecting forests from damage by insects was gradually realized.

## HISTORY OF FOREST ENTOMOLOGY IN THE SOUTH

**RESEARCH:** It is interesting to note that the science of Forest Entomology in the United States had its real beginning in the South when Dr. Hopkins conducted his early studies on the southern pine beetle in West Virginia about 1890. Since then many well-known forest entomologists have worked there; they include Balch, Beal, Blackman, Craighead, and others. Most of the early work concerned taxonomic studies of our

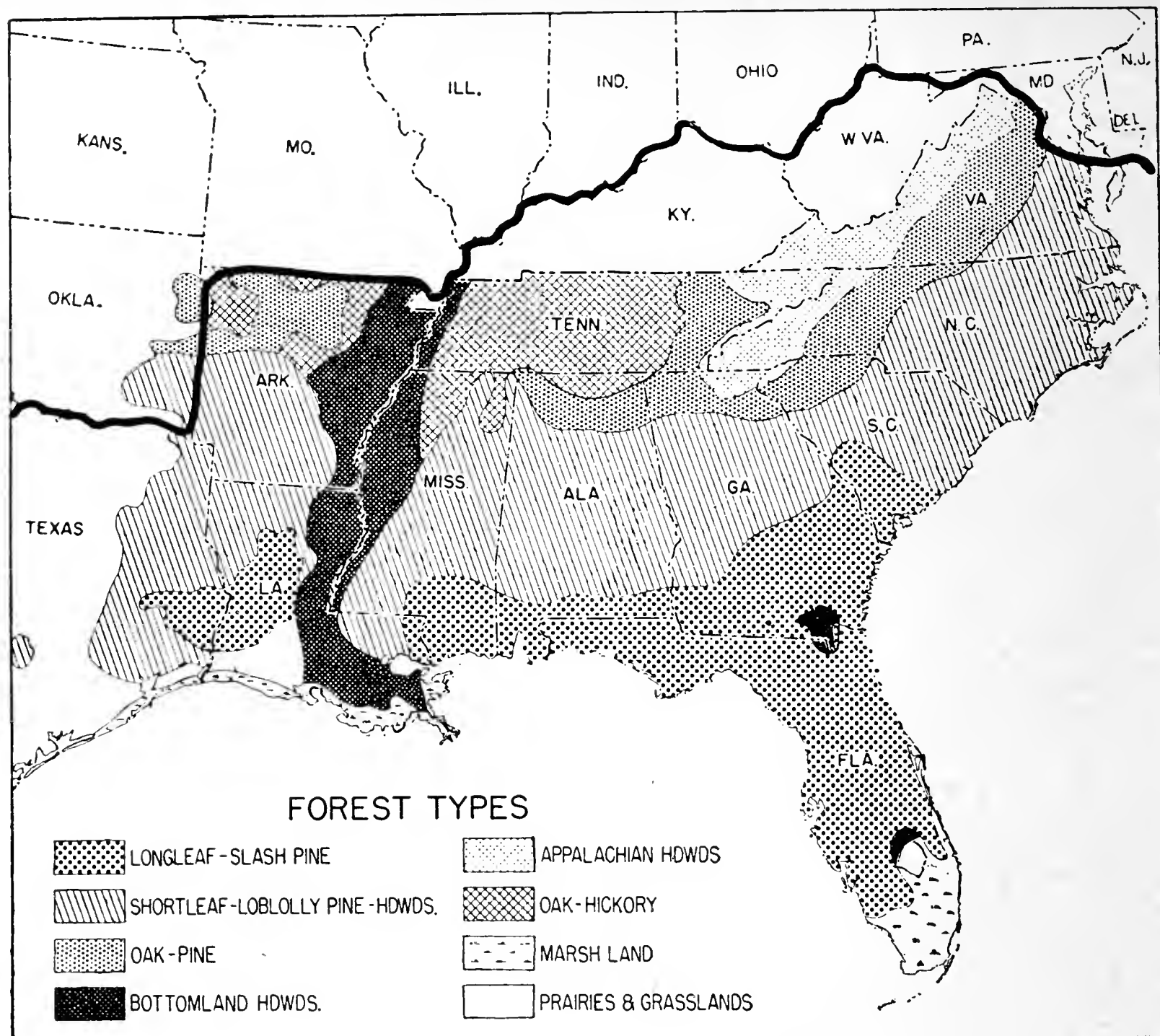


Fig. 1. A map of Southern United States showing predominant forest types. (Forest types in West Virginia and Kentucky are not shown.)

forest insects. Essential information on life histories, habits, and direct control was obtained for the most important insects.

However, the total effort in study and research compared to other parts of the country was very small. During the early part of the century research was centered around Falls Church, Virginia; then at Asheville, North Carolina. About 1930 permanent personnel were assigned at Asheville; in 1935 a laboratory was opened at New Orleans, Louisiana. But until the late forties these laboratories were intermittently manned by one or two scientists, and much of their time was spent on insects affecting forest products.

Genuine interest in forest insects started about 1945 when a series of epidemics began to appear. Damage by sawflies, bark beetles, and miscellaneous defoliators aroused intense interest. It is doubtful that this interest would have come about but for significant changes in the field of forestry. Stands were being placed under intensive management, competition in the field was becoming strong, and values of the forest were climbing. Progress in the practice of intensive forestry since 1945 has been almost unbelievable. One might use the employment factor to illustrate progress: in 1945 one well-known paper company employed less than 5 professional foresters; now it employs over 50. In 1945 there were 10 consulting foresters in the whole South. Now there are about 225.

How did forest entomologists meet this new and great demand for information, for assistance and advice? Primarily, it was necessary to take information developed in other parts of the country and modify it for use in southern forests. An alternative approach was short-term, or what we commonly call "quickie" research. This tool has

been a very valuable one. In general it has centered around direct control of insects through the use of insecticides. The development of synthetic organic insecticides had a profound influence upon research in forest entomology in the South as elsewhere. With the introduction of DDT in 1942 came a decade of concentrated research on insecticides and direct control, much of it "quickie" in nature. The contributions during this period were invaluable. But it was inevitable that new problems would be created; and that fundamental forest insect research programs, especially in the South with its very small number of professional forest entomologists, must suffer.

Thus, our knowledge of the life history and behavior of forest insects is limited; so is our knowledge of the relationship between the insect, its host and environment. Research funds, however, have begun to increase and our research staffs show slight increases.

**SURVEYS:** Passage of the Forest Pest Act in 1947, which made possible survey and control activities, has added immeasurably to progress in Forest Entomology. Its effect was vastly greater in the South than in any other part of the country, for until passage of the Act, there was no existing forest insect survey program as there was in the North and West. There had never been a cooperative large-scale control program. In the last six years, detection programs have been organized involving state, federal, and private industry cooperation; each year at least 4,000 foresters have attended training sessions to become acquainted with identification of insects, their detection, and control; forest pest committees have been set up in a number of the states; state forest pest laws have been passed and states and industries have been encouraged to employ forest entomologists. (Within the past few years two paper companies and four State Forest Services in the Southeast have employed entomologists; others are considering such action.) An indirect effect of these activities, but a very valuable one, has been to stimulate in the average forester an interest in and appreciation of entomological research and research needs. Until research develops effective means to prevent or forecast destructive insect outbreaks, the survey program, particularly detection programs, will play an important part in keeping losses to a minimum.

## REVIEW OF INSECT PROBLEMS, RESEARCH AND CONTROL ACTIVITIES

Reliable loss figures to illustrate damage caused by forest insects have been extremely difficult to obtain until recently. The recently issued report of the Timber Resource Review estimated that during 1952 the total losses for all insects in the Southern States, not including Virginia and West Virginia, were about 108 million cubic feet growth loss and 403 million board feet mortality loss. Since that time our more intensive survey program has revealed that annual mortality for known bark beetle outbreaks alone approaches 400 million board feet; unknown mortality-loss probably exceeds that figure.

Data on the destruction caused by wood products insects are equally difficult to obtain. We can only say that the cost runs into many millions of dollars annually.

## WOOD PRODUCTS INSECTS

Probably the greatest advances in forest entomology in the South have been in wood products insects. Monumental research on taxonomy and habits of termites of the world was conducted by Dr. T. E. Snyder while he was in the South. Equally significant contributions have been made by others in every aspect of the biology and control of subterranean termites.

Most of the research on powder-post beetles of the United States was conducted in the South. Intensive studies on the biology of *Lyctus* spp. were followed by research on control by means of sanitation, heat treatment, starch depletion, fumigation, and application of chlorinated hydrocarbons. The latter is giving highly effective results in terms of immediate control and long-time protection.

There are a number of other powder-post beetles which do a great deal of damage. Research on these has been limited. *Hylotrupes bajulus* is becoming a very important problem. Among the Anobiidae, Bostrichidae, and Curculionidae are species whose damage is more or less severe.

One of the most complete pieces of research was conducted on biology and control of ambrosia beetles. In control studies every aspect of formulation, application, and persistence of insecticides was investigated. Results showed that  $\frac{1}{2}$  per cent gamma BHC in oil sprayed on logs would protect them 3 to 4 months; a .075 per cent concentration applied as a water emulsion dip treatment protects lumber until it is too dry for attack. These studies provided a background of information which proved to be of value in the control of other forest insects.

In response to requests from the pulp and paper industry, studies were begun in 1945 in an effort to prevent deterioration due to bark beetles and borers of pulpwood, which in the South is normally stored for 3 to 4 months with bark intact. Treatment with BHC in oil proved very promising but it was not sufficiently effective at millyards, where insect populations are abnormally high; also it is difficult to adapt to mill practices. Improvement of the treatment or changes in storage operations may provide a solution to the problem.

### FOREST INSECTS

**BARK BEETLES:** Pine bark beetles are generally considered the most destructive forest insects in the South. Of these, the southern pine beetle, *Dendroctonus frontalis*, is usually the most serious. Epidemic outbreaks have been recorded periodically since 1850. In its endemic status the beetle is very obscure and sometimes impossible to find. It attacks all ages and all species of pine within its range. When conditions are favorable for epidemic outbreaks, beetle populations build up very rapidly, and areas of timber from  $\frac{1}{4}$  acre to 100 acres may be killed in a short time.

Since 1945, there has been a gradual increase in outbreaks of the beetle until at present they are occurring in most parts of the South. Over 100 million board feet have been killed annually during the last 5 years in known outbreaks.

The engraver beetles, *Ips calligraphus*, *Ips grandicollis*, and *Ips avulsus*, are the most common of the bark beetles. During so called "normal" periods this group of bark beetles is secondary. Beetles can always be found attacking the occasional injured, weak or felled trees. However, in recent years it has become epidemic in its activity. In most instances woods fires, storm damage, or some other breeding condition is required to begin the population build-up; beetles then move rapidly into apparently healthy trees even before all injured trees are infested. Such abnormal situations are not always required, however; beetles may attack trees only in groups of 1 to 3 but these kills occur in much greater frequency than during "normal" periods. In 1955 an estimated 200 million board feet were killed by *Ips* spp.

The engraver beetles and the southern pine beetle have short life cycles and produce 4 to 6 generations per year. The latter, however, has a much greater biotic potential, produces many more beetles, and kills many more trees during a season.

Control of these beetles usually consists of rapid salvage, lopping of tops, and general sanitation. Salvage is often practicable because of many portable sawmills and the heavy demand of the large pulpwood industry. When it is impracticable to salvage, a residual penetrating spray is applied to felled trees. Many series of screening tests conducted in various parts of the South proved that  $\frac{1}{4}$  per cent gamma BHC in oil is the most effective insecticide treatment.

Until 1949, the black turpentine beetle, *Dendroctonus terebrans*, was always regarded as secondary; no epidemic outbreaks were on record, and tree mortality was very rare. Since that year, it has been killing trees throughout the South. It was first observed following cutting operations; then, in 1951 it was found killing trees following the southern pine beetle outbreak in Texas, and in the same year it caused pine mortality in the naval stores region of Florida. Damage during 1955 was estimated at 50 million board feet; there was probably an equal or greater loss to the naval stores industry due to loss of gum trees and reduction in size of the naval stores crop through fear of the beetle's activities.

The beetle infests all species of pine in the South, confining its attack to the base of the trees. Subsequent attack on roots destroy their function and contribute to the tree's death. The beetle has a life cycle of 3 to 4 months.



Studies on direct control involving many chemicals and formulations have resulted in the development of treatments to prevent breeding in stumps and to protect high value specimens such as naval stores trees and seed trees and those used in tree improvement programs such as genetically superior individuals. A 1 per cent gamma concentration of BHC in fuel oil, applied as a coarse spray, was found to be the most effective treatment.

**DEFOLIATORS:** In the South, there are at present no defoliators as destructive as the spruce budworm, the Douglas-fir tussock moth, and the larch sawfly. We have a great many species but so far as we know their injury seldom causes direct mortality. In recent years, however, there has been increasing concern about the possible effect of defoliation on tree growth or susceptibility to attack by other insects. Probably the first occasion of concern was in 1947 when the loblolly pine sawfly, *Neodiprion taedae linearis*, defoliated loblolly pine of all ages in over 1½ million acres of forest land in southern Arkansas. Observations over several years revealed no appreciable mortality resulting from this defoliation, but studies showed a severe growth loss of 20 million board feet during the peak year. The insect has since been found in northern Louisiana and Texas.

There are, in the South, at least seven other species of sawflies about which little or nothing is known. Some of these might potentially be more serious than the species discussed above because they defoliate in late summer and fall when refoliation is poor and trees are predisposed to lethal attack by bark beetles.

Space does not permit discussion of the many other defoliators considered to be serious in their effect on trees. They include such species as the cypress looper, the cypress leaf beetle, the elm spanworm, the fall cankerworm, the forest tent caterpillar, and the oak leaf miner. Periodically, areas of a few hundred to many thousand acres are defoliated. The effect of their damage has never been fully studied but in some instances obvious effects have been noted such as stand deterioration and, in the presence of adverse growing conditions, mortality.

**PALES AND OTHER REPRODUCTION WEEVILS:** Until a few years ago the Pales weevil, *Hylobius pales*, was considered an insect problem of the Northeast only, where it girdled and killed young white and red pine around logging areas and similar points of attraction. There are no published records of injury to southern pine previous to 1940. That year it was reported causing serious damage to pine in recently cutover areas on the Duke University Forest. In 1948 near Hodge, Louisiana, the weevil virtually wiped out a pine plantation established in an area which had been burned and salvaged. At this time, another weevil, *Pachylobius picivorus*, was collected. Since then, reports of damage by these insects have been increasingly common as planting programs have been enlarged. The recent development in management practices to cut and plant pine has also increased losses by the weevils.

The method of control in the Northeast in past years was to delay planting for three years, until the beetle completed its activities and left the area. This method has been largely rejected in the South because of heavy growth of hardwood reproduction on many sites during this waiting period. Thus far, insecticides have offered the best promise of quickly developing a method of control; indirect methods might be most effective in the long run, but their development will require considerable time.

A very promising form of control has been developed which consists of dipping seedlings in a 2 per cent water emulsion of aldrin. At a cost of about 15 cents per thousand, over 80 per cent of the seedlings can be protected during the period when beetles feed. Preliminary tests of spray solutions and dry granular insecticides, for use under special conditions, likewise show promise.

**PINE MOTHS:** The pine moth, *Rhyacionia frustrana*, is familiar to foresters in the South. Damage by this insect, which consists of mining out buds and shoots, usually causes 6 to 8 inches growth loss per year for 6 to 10 years. On poor growing sites the damage may cause dwarfing. Injury to loblolly and shortleaf pines has been so serious in some areas that these pines are being replaced by other species.



Reasonably effective control measures have been developed in recent years but have not been accepted because cost of control usually exceeds the losses. Two applications of a 1 per cent water suspension or emulsion of DDT to infested trees, accurately timed to kill the larvae of the first two spring generations, has given a high degree of control. Spraying by aircraft was studied briefly against another species of tip moth some years ago but proved unsatisfactory. It should be more thoroughly investigated in the South. Application of concentrated sprays with mist blowers also needs study as a possible inexpensive method of control.

### CONTROL OF INSECTS BY INDIRECT MEASURES

In the above review of various destructive insects, only direct control measures have been discussed as each pertains to the particular species concerned. This discussion of indirect control applies broadly to all species.

Generally speaking, before we can develop sound methods of indirect control in the South, we must have more information on the relationship of the various insects to their environment. For example, in any discussion of the epidemiology of bark beetles, drought is always listed as the major factor. Yet abundant rainfall does not always end epidemics. On the other hand, epidemics have ceased completely while drought continued. In the case of the southern pine beetle there are many drought areas, having a past history of severe epidemics, that are presently unaffected by the beetles. It appears likely that a combination of factors or conditions — biology of the beetle and its natural enemies, climate, forest stand density and volume, and the soil — are involved. Discovery of the nature of this combination may someday lead to development of effective methods of biological or silvicultural control.

There are instances when the possibilities of control by simple management practices appear so obvious that basic information seems unnecessary; for example, control of black turpentine beetle by temporary cessation of naval stores; or control of *Ips* by stopping summer cutting. But these methods do not conform to the economy of our forest industry; they are expensive — and in effect, they constitute an attempt to escape the problem rather than solve it. Basic information will lead to more effective control through management and biological and silvicultural methods.

The need for fundamental study applies equally to defoliators. The possibilities that lie in biological control through the use of natural enemies are well known to all of us. Less well known, however, is the effect of climate on the condition of the host; for example, as it relates to injury by defoliation. The numerous epidemic outbreaks of different species of defoliators during recent years suggest an environmental influence; study of the relationship of the insect to its environment may reveal strong climatic or site influences which could lead to development of silvicultural control techniques.

In the control of the Pales weevil there seem to be several possibilities of control by management — proper timing of the harvest cut to reduce beetle breeding, and cutting during high seed years to ensure an adequate seedling crop despite weevil damage. These possibilities, however, can be satisfactorily tested only when fundamental information is available.

Although there will always be a place for the application of insecticides and similar direct control measures, long-time protection will come only through natural methods of control which will require painstaking basic research.

### FUTURE PROBLEMS IN FOREST ENTOMOLOGY

The above review of forest entomology in the South has been presented by describing some of the better known problems. However, there are many problems which are only being explored at present. Also, if we look into the not-too-distant future we can see new problems developing.

In the former category are the insects which affect hardwoods. As previously indicated, the South's forest economy has largely revolved about pine. There is now a gentle swing toward hardwoods and it is the writer's opinion that this move will gain momentum very rapidly in the next decade. Interest in insect damage is clearly

evident. Recent exploratory studies in Kentucky reveal that 75 per cent of oak lumber is severely damaged by borers. Management studies recently established in Georgia show heavy borer damage even in young saplings. The task of determining the insects causing the injury, their life histories and the conditions favoring their activity will be a formidable one; devising control measures will be equally challenging.

Interest in the field of forest genetics in the South has mounted rapidly in the past five years. Forest entomology must progressively play an important and essential part in many of the developments. Already insect problems have arisen. Scions of slash pine grafts are highly susceptible to attack by a bark beetle, *Pityophthorus pulicarius*, and it has become necessary to develop control measures. In making pollen crosses, certain cone insects cause a high mortality of seed; studies have begun to determine ways of controlling this loss. In seed orchards, pine tip moths are expected to lower cone production, as they destroy the flower buds of the low-growing trees. Current examinations of seed source studies suggest that susceptibility or resistance to insect attack may be related to seed source. There is evidence that certain trees exhibit resistance to insect attack, as in the case of bark beetles. The idea of inbreeding trees with resistance is not a particularly hopeful one to many entomologists but its possibilities must not be overlooked.

Looking into the future, as the forest industry of the South continues its enormous strides, one can see possibilities of many new problems developing unless they are anticipated and preventive measures taken. The tremendous southern planting program (475 million seedlings planted in 1956, and 1 billion predicted for 1970) will bring insect problems in the numerous new nurseries needed to produce planting stock. Later will come different problems associated with plantations; still later the problems of the young and the maturing stand. In considering the future, one might contemplate with alarm the vast plantings of pure even-aged stands of pine and the danger that exists from attack by some of the primary insects discussed before. That is, unless we have confidence in our ability to develop, in the near future, the biological, silvicultural or management methods of preventing insect outbreaks. In our attempts to develop and establish such methods of control we must have full cooperation of forest managers. For the southern forest with its rapid growth and short rotation encourages frequent change in management systems. Such changes could jeopardize silvicultural control measures. Foresters must realize too that the environmental changes that go with intensive management — road building, draining, prescribed burning, clear cutting, etc., may have adverse effects on the stand with respect to susceptibility to insect attack.

Though the future presents many problems, there are signs that these will be met successfully. Entomology is being recognized as an integral part of forest protection. Insect detection programs are taking effect and every year sees more foresters in the woods to aid in the program. Aerial survey techniques in the South are being improved through research. And, perhaps most important is the fact that foresters are recognizing the value of all these efforts — the fundamental as well as the "quickie" research, and the survey as well as the service activities of the entomologist.

## DISCUSSION

C. M. BAETA NEVES. Je vous pris la gentillesse de m'informer si vous avez noté à l'Amérique quelques variations de résistance des pins aux attaques des insectes avec le procédé de gemmage à l'acide en relation avec le procédé ancien.

R. J. KOWAL. There has been no study to determine the fact but we have not observed any correlation. We would expect less attack on bark-streaked acid treated trees because the tree is not as severely injured as in the deep wood streaking treatment.

V. BUTOVITSCH. (1) In what part of the United States does *Hylotrupes bajulus* occur? (2) What is the concentration of BHC which is used for spraying of timber against *Dendroctonus* spp.?

R. J. KOWAL. (1) We know that it occurs throughout the eastern United States and is becoming increasingly serious here. It is found principally in buildings. It has been recovered in other parts of the country, such as in Douglas-fir timber in the West.

In recalling my study of literature on the subject, my impression is that the insect is generally distributed throughout the country but much more serious in the eastern United States. (2) 0.25% gamma BHC against *Ips* spp. and *Dendroctonus frontalis* to control the brood; 1% gamma BHC against *Dendroctonus terebrans* to prevent attack and to control existing attack to save the living attacked tree.

J. D. BLECHLY. (1) I would like to ask Mr. Kowal whether the measures to prevent *Lyctus* infestation in green lumber recommended by Christian by using borax or 2% micro-fine sulphur are still in use or whether newer measures are now available. (2) In the case of seasoned lumber in tests at Princes Risborough we have not found pentachlorophenol solutions in fuel oil very effective in preventing *Lyctus* attack. What measures are now recommended? (3) With reference to slide showing *Lyctus* damage in an ash handle, are any standard preventive measures in force as we experience trouble in England with importation of infested ash handles.

R. J. KOWAL. (1) In preventing *Lyctus* infestation of green lumber, borax and micro-fine sulphur are no longer recommended. We have found that a 10-second dip in a cold-water emulsion containing either 5% DDT or 0.5 gamma isomer of benzene hexachloride are much more effective. These formulations can be combined with commonly used sapstain preventives, so that one trip through a dipping vat will protect green lumber against both stain and beetles. This is a surface treatment, however; another treatment is needed after the wood is planed. (2) Your comment that pentachlorophenol solutions in fuel oil were not very effective in preventing *Lyctus* attack in tests at Princes Risborough is very interesting. We have had similar results in our tests here. These studies have shown that a 3-minute cold dip in light oil solutions of 5% DDT, 5% toxaphene, 2% chlordane, or 0.5% lindane will prevent attack for at least 5 years; we expect much longer protection. (3) There are no regulations in this country which require that wood susceptible to *Lyctus* infestation be free of attack.

# Foliage and Shoot Production of Tamarack as Factors in Population Studies of the Larch Sawfly, *Pristiphora erichsonii* (Hartig)<sup>1</sup>

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## ABSTRACT

This paper presents a preliminary investigation on developing a foliage sampling method for estimating tamarack foliage production as a factor in population studies of the larch sawfly. Weight of foliage per fascicle differed between branch sections for some branches, but showed no consistent trends. Fascicle weight was less in the upper portions of the crown than in the lower, and increased as the season progressed. Weight of foliage per branch differed between crown levels and had large intra-crown level variability; adjustment for branch size effected a reduction in the coefficient of variation. The ratio of shoots to foliage differed between trees and was greatest in the upper portions of the crowns. Little relationship existed between mean shoot length and mean fascicle weight. Foliage length was closely related to foliage weight and a bimodal intra-fascicle frequency distribution of needle length was similar in shape for a wide range of fascicle weights. Whole branch samples of foliage, adjusted for branch size, are the most promising survey method for estimating foliage production, and can be used in conjunction with estimates of sawfly populations. Estimates of foliage and shoot production on an area basis is the most promising method for life table studies. This method is most useful since populations of different stages of the larch sawfly can all be given on this basis.

## INTRODUCTION

The larch sawfly, *Pristiphora erichsonii* (Hartig), has been the most common insect attacking tamarack, *Larix laricina* (Du Roi) K. Koch, in the Prairie Provinces for the past decade. The most recent outbreak started to decline by 1953 in many areas after several years of severe attack (Lejeune and Hildahl, 1954). Several factors have contributed to this decline, but at the present time it is difficult to establish which are the most important. Life tables would provide a method for evaluating the importance of factors governing fluctuations in larch sawfly populations, but before satisfactory life tables can be developed it is necessary to develop a technique that will make it possible to relate sawfly populations to foliage production.

The amount of foliage available to the larvae as food is one factor undoubtedly responsible for limiting the size of the larch sawfly population a tree or stand will support. Both the amount of foliage and number of new shoots decrease after severe attack by the insect, and this condition may continue to the point where lack of oviposition sites and decreased foliage production become factors in controlling larch sawfly populations (Lejeune, 1951, 1955).

The study of the foliage and shoot production of tamarack throughout a sawfly outbreak should provide information on the effect of the insect upon its host, and of the host upon the insect. Foliage sampling methods must be developed before such a study can be successfully undertaken. This paper presents the results of the preliminary work initiated in an attempt to develop a suitable sampling technique for estimating foliage production of tamarack. Variation in foliage production was studied to determine which factors affect the weight of foliage produced.

The field work for this study was conducted in the Whiteshell Forest Reserve in southeastern Manitoba in 1954 and 1955. Two study plots were established in even-aged stands that were subsequently lightly defoliated. Each plot consisted of eight uniform trees with well-formed crowns. The average height of the trees was about 40 feet in Plot I and 35 feet in Plot II, with mean ages of about 35 and 30 years respectively. The width of the 1954 annual rings at the 1-foot level averaged 0.06 inches for the

<sup>1</sup>Contribution No. 367, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.



sample trees in Plot I, and 0.03 inches for those in Plot II. The annual rings on suppressed or severely defoliated trees are often less than 0.01 inches in width.<sup>2</sup> The sample trees, therefore, show little increment loss in 1954 that could be attributed to attacks by the larch sawfly.

## METHODS

A random sample of three trees was selected from each plot. The heights of the sample trees were measured with an Abney level, and estimates made of the crown depth. The crown depth for each tree was divided into 5-foot intervals (hereafter referred to as crown levels), starting at the top of the tree. Random number tables were used to determine the location, by height and cardinal points, of four branches to be sampled from each crown level. Extension pole pruners with a clamping device similar to that used by Morris (1955) were used to remove the branch nearest the randomly selected position.

Two branches were removed from each crown level during a period of three weeks, beginning one week after foliage growth appeared complete. Each branch was placed on a marked board in the field laboratory and measurements taken of the foliated length and foliated width at the widest point. The branch was cut at 1-foot intervals along the arcs of concentric circles, after aligning the tip of the branch with the nearest arc. A random number between 1 and 100 inclusive was then drawn for each section of the branch. The numbers of fascicles and new shoots per section were recorded. While counting, every hundredth fascicle was removed intact, beginning the sequence with the fascicle corresponding to the random number selected. Since the number of fascicles per branch section was seldom an even multiple of 100; if the random number was less than the number of fascicles, the given fascicle was collected; if the random number exceeded the number of fascicles, no sample was taken. Each fascicle was placed in a small vial and stored in a desiccating cabinet.

The two remaining sample branches in each crown level were removed after terminal growth had apparently ceased and treated in the manner described above. The occurrence of some defoliation occasionally necessitated deviating from the random number series. In these instances the next sound fascicle past the designated one was chosen, returning, if possible, to the random number series at the next designated sample fascicle. A 10 per cent sample of new shoots was also taken from each section, using a procedure similar to that for selecting the foliage samples. The new shoots, with their basal fascicles of foliage<sup>3</sup>, were placed in individual vials and stored with the rest of the foliage. The remaining shoots from each branch section were placed in paper bags. All shoots without oviposition scars were later measured.

The trees were felled after all foliage sampling had been completed, the height measurements were checked, and disks were taken at the 1-foot level. The width of each annual ring was measured to the nearest one-hundredth inch along three radii.

In addition to the above foliage samples, 30 fascicles were selected from each of three groups of trees as follows:

Group I from two young vigorous 3-foot trees;

Group II from a tree in the same stand as Plot I; and

Group III from two widely separated mature trees with luxuriant foliage. The fascicles were not selected completely at random, but were chosen to represent a wide range in fascicle length.<sup>4</sup> The needles were plucked while still fresh, and each needle measured separately. The measured foliage from each fascicle was placed in vials and stored in a desiccating cabinet.

Prior to oven-drying the needles were removed from the spurs, and the shoots were relaxed so that the foliage of the basal fascicle could be separated from that on the shoot. All the foliage was then oven-dried at 105°C. for 48 hours before weighing.

<sup>2</sup>L. D. Nairn, 1956. Personal communication. Forest Biology Laboratory, Winnipeg, Manitoba.

<sup>3</sup>The term basal fascicle is used to differentiate the whorls of needles at the base of the shoot from the needles on the new shoot.

<sup>4</sup>The term fascicle length refers to the maximum length of the needles in a fascicle, measured from the tips of the current year's bud scales.



The needles were stored in a desiccating cabinet to prevent moisture absorption in the interval between drying and weighing.

In 1955 a fast-growing and a slow-growing tree were selected for a supplementary study of factors that might influence foliage weight. Thirty-two branchlets were tagged on each tree. Eight uniform fascicles were selected on each branchlet and the spurs marked with red model-aircraft dope. Eight treatments, representing all combinations of three factors at two levels, were randomly assigned within each branchlet. The factors were: early versus late season sampling; morning (8:00 to 9:30 A.M.) versus afternoon (3:30 to 5:00 P.M.) sampling; and plucking the needles while fresh versus leaving them on the spur until dry. The foliage was handled as in 1954, except that it was placed in a humidity chamber for relaxing, prior to oven-drying and weighing. This facilitated plucking the needles from the spurs.

### FOLIAGE WEIGHT

The foliage production of tamarack may be expressed either as an index or as an absolute quantity, depending on the objectives of the study. Since this study was exploratory in nature, it seemed advisable to examine a number of measures of foliage weight. Foliage variation will therefore be discussed under the following headings: weight per fascicle; weight per branch; ratios involving foliage weight; and foliage weight and shoot length.

#### WEIGHT PER FASCICLE

Several factors could influence the amount of foliage per fascicle. Those that were studied include location of the fascicle within the branch, location of the branch within the crown, sampling date, and variation between trees.

#### INTRA-BRANCH VARIATION

The sizes of fascicles often vary between different sections of the same branch. To test for any intra-branch trends in foliage weight, an analysis of variation between and within sections was conducted for each branch. More significant differences were found than could be attributed to chance alone, so it must be assumed that real differences exist between the weight of foliage per fascicle from different sections of the same branch. There is an indication that the fascicle size increases from the distal to the basal section of the branch, but this trend is not consistent. The appearance of the foliage on the branches seemed to indicate a marked reduction in the amount of foliage produced on fascicles that had been defoliated during the previous year. If this assumption is correct, a large part of the intra-branch variation in foliage weight may be attributable to the larch sawfly.

Since no consistent trends were found, the data for each two-branch sample were pooled before continuing the analysis.

#### INTER- AND INTRA-TREE VARIATION

Each sample was classified according to tree number, crown level, and date of sampling. To test for the presence of interactions between these classifications, the normal equations were solved for estimates of the parameters concerned. The sum of square removed under the hypothesis of no interaction was then calculated for each plot, following the standard procedure (Kempthorne, 1952). The results of the tests are shown in Table I. The *F* values are significant at the .01 level for both plots, indicating the presence of interactions between the classifications.

The effect of each of the factors upon the weight of foliage was tested for each plot. Analyses were conducted for variation between and within each classification. These tests are probably insensitive, but do not make any assumptions about interactions. The calculated *F* values are shown in Table II.

The variation between trees was significant at the .01 level for Plot I but not for Plot II. This shows that there may be considerable variation in fascicle size between trees, even when the trees appear similar. The differences would probably be much larger in a typical stand, where a number of tree types often occur.

TABLE I— Analysis of Variance used in Testing for the Presence of Interaction Between Trees, Crown Levels, and Dates of Sampling.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F
Plot I				
Fitting (u, t <sub>i</sub> , c <sub>j</sub> , d <sub>k</sub> )*	9	183910.91		
Difference	22	1616.00	73.445	2.051**
Fitting (u, t <sub>i</sub> , c <sub>j</sub> , d <sub>k</sub> ) and interaction	31	185526.91		
Within cells	1199	42949.61	35.821	
Total	1230	228476.52		
Plot II				
Fitting (u, t <sub>i</sub> , c <sub>j</sub> , d <sub>k</sub> )*	9	234030.35		
Difference	22	2476.47	112.567	2.474**
Fitting (u, t <sub>i</sub> , c <sub>j</sub> , d <sub>k</sub> ) and interaction	31	236506.82		
Within cells	1150	52322.46	45.498	
Total	1181	288829.28		

\*u = over-all mean; t<sub>i</sub> = tree effect (i = 1,2,3); c<sub>j</sub> = crown level effect (j = 1, —, 5); d<sub>k</sub> = date of sampling effect (k = 1,2).  
\*\*Throughout this paper a single asterisk after an F or an r value indicates significance at the .05 level, and a double asterisk indicates significance at the .01 level.

TABLE II — Tests for Factors Affecting the Weight of Foliage per Fascicle.

Analysis	Plot I	Plot II
Between trees	F <sub>2,1227</sub> = 11.85**	F <sub>2,1178</sub> = 2.41
Between crown levels	F <sub>5,1224</sub> = 10.32**	F <sub>5,1175</sub> = 6.05**
Between sampling dates	F <sub>1,1228</sub> = 4.46*	F <sub>1,1179</sub> = 42.94**

Differences between crown levels were significant at the .01 level for both plots. The mean oven-dry weights in milligrams of foliage per fascicle from different portions of the crown were as follows:

Plot	Distance from top of tree in feet						
	0 - 5	5 - 10	10 - 15	15 - 20	20 - 25	25 - 30	30 - 35
I	*	11.2	10.1	12.4	13.6	13.6	12.6
II	11.9	13.6	12.9	15.0	14.9	14.7	—

\*Errors in Abney level measurements precluded sampling.

In both plots the weight of foliage per fascicle is less in the upper portions of the crown than in the lower portions.  
Differences between sampling dates were significant at the .05 and .01 levels for Plot I and II respectively. The mean foliage weights per fascicle for early and late sampling were 11.8 and 12.5 mg., respectively, for Plot I and 12.9 and 15.5 mg., respectively, for Plot II. These differences could be important when considering the development of a foliage sampling method, since the sampling would have to be conducted before defoliation takes place. This would limit the sampling to a period corresponding to the early sampling dates.

SEASONAL VARIATIONS IN 1955

It has been shown that the mean weight of foliage per fascicle in 1954 was greater in late summer than in early summer. The 1955 experiment was initiated to test the

annual consistency of this difference. The data were also used to obtain information on the possible effect of leaving the foliage on the spurs to dry instead of plucking it while fresh, and of morning versus afternoon sampling. The effects and interactions were tested by analysis of variance, as shown in Table III.

TABLE III — Analysis of Variance for Testing Hour of Sampling, Date of Sampling, and Method of Sampling Effects and Interactions for Fast Growing and Slow Growing Trees, Based on Weight of Foliage per Fascicle.

Source	Degrees of freedom	Fast-growing		Slow-growing	
		Sums of squares	F	Sums of squares	F
Blocks	31	5301.00		2950.65	
Treatments	7	1246.29		363.89	
Effects and interactions					
H†	1	143.70	1.99	18.60	1.23
M	1	214.99	2.98	46.41	3.07
H x M	1	7.91	0.10	0.10	0.01
D	1	744.61	10.30**	281.82	18.63**
H x D	1	83.95	1.16	0.21	0.01
M x D	1	19.91	0.28	10.81	0.71
H x M x D	1	31.22	0.43	5.94	0.39
Error	217	15682.36		3283.19	
Total	255	22229.66		6597.73	

†H = hours of sampling; M = methods of sampling; D = dates of sampling.

Differences between the early and late sampling periods are again significant at the .01 level, indicating that these differences are normal, and not due to an unusual season. The mean oven-dry weight in milligrams of foliage per fascicle for the different main effects on the fast-growing and slow-growing trees were:

Appearance of tree	Season		Time of Day		Method of handling	
	Early	Late	Morning	Afternoon	Plucked	On spur
Fast-growing	36.0	39.5	37.0	38.5	36.8	38.7
Slow-growing	18.7	20.8	19.5	20.0	19.3	20.2

The results show that the means for morning and afternoon sampling, and for the two methods of handling, are not significantly different, but they may represent real differences, since they are consistent for both the fast-growing and slow-growing trees. However, they are not of sufficient magnitude to affect materially the accuracy of any foliage production estimates. It is possible that a table of conversion factors could be developed to adjust foliage weights for samples taken at different dates, and thus eliminate seasonal differences.

WEIGHT PER BRANCH

The weight of foliage per branch was estimated by the formula

$$W_j = \sum_{i=1}^{n_j} \bar{x}_i n_i \quad , \text{ where}$$

- W<sub>j</sub> = the estimated weight of foliage for branch j;
- $\bar{x}_i$  = the mean weight per fascicle for the i<sup>th</sup> section of the branch;
- n<sub>i</sub> = the number of fascicles in the i<sup>th</sup> section<sup>5</sup>; and
- n<sub>j</sub> = the number of sections for which foliage samples were taken for branch j.

<sup>5</sup>If no foliage samples were taken for a branch section, the number of fascicles in this section was added to the number in the nearest sampled section before estimating the foliage weight.

These figures were used to obtain an estimate of the variation in weight of foliage per branch. However, these should be considered as provisional estimates, since the foliage weights are estimates and only six trees were sampled. Analyses of variance were conducted for each plot and confined to five crown levels. The results of these analyses are shown in Table IV.

TABLE IV — Analyses of Variance for Testing Tree, Crown Level, and Date of Sampling Effects and Their Interactions, Based on Estimated Weight of Foliage per Branch.

Source	Degrees of freedom	Plot I		Plot II	
		Mean square	F	Mean square	F
Trees	2	586.38	2.31	733.89	2.65
Crown levels	4	1157.10	4.56**	1466.38	5.30**
Dates	1	252.97	1.00	50.79	0.18
Trees x crown levels	8	189.28	0.75	284.75	1.03
Trees x dates	2	1304.26	5.14*	283.58	1.02
Crown levels x dates	4	484.30	1.91	304.91	1.10
Trees x crown levels x dates	8	241.18	0.95	295.85	1.07
Error	30	253.66		276.94	

Crown level differences are significant at the .01 level, indicating that any foliage sampling method should use stratification by crown levels. There are no significant differences between trees or between dates of sampling. The tree-by-date interaction is significant at the .05 level in Plot I, but examination of the data suggests that this may be attributed to the vagaries of sampling. Both of the error mean squares are large, so large samples will probably be needed for accurate estimates.

### RATIOS INVOLVING FOLIAGE WEIGHT

The high variation in the amount of foliage per branch would limit the value of an index based on this figure. Any foliage sampling that might be conducted on an extensive scale would have two objectives: (1) to study trends in foliage production through the course of an outbreak; and (2) to study trends in the number of new shoots in relation to the amount of foliage.

### WEIGHT AND BRANCH SIZE

Morris (1954, 1955), working with balsam fir, expressed spruce budworm populations on a "branch area" basis to reduce variation attributable to branch size. Tamarack branches are much more irregular in form than those of balsam fir, but Morris' work suggested the possibility that variation in foliage weight per branch might be reduced by adjusting for branch size. The correlation between "branch size" (foliated width by foliated length) and estimated foliage weight were calculated for each tree. The *r* values obtained for Plot I were .791, .759, and .679 with 17, 21, and 18 degrees of freedom. Those for Plot II were .892, .861, and .822, with 22, 18 and 18 degrees of freedom. Although the *r* values are based on estimated foliage weights, all of them are high. The amount of foliage per branch was therefore expressed as the number of grams of foliage per unit (1000 square inches) of "branch size". An analysis of variance was conducted for each plot, as shown in Table V.

Tree differences are significant at the .01 level for Plot I, but are not significant for Plot II. Crown level differences were also significant at the .01 level for Plot I, but the presence of a significant tree-by-crown level interaction shows that these differences do not follow the same trend for all trees. Differences between dates of sampling are also significant at the .05 level. Apparently the correction for branch size removed the masking effect of the variation in branch size.

The error mean square for the index of foliage abundance is considerably smaller than for the weight of foliage per branch, although the differences in the means are not

TABLE V — Analyses of Variance for Testing Tree, Crown Level, and Date of Sampling Effects and Their Interactions, Based on Estimated Foliage Weight per Unit of "Branch Size".

Source	Degrees of freedom	Plot I		Plot II	
		Mean square	F	Mean square	F
Trees	2	95.55	4.19**	71.74	1.76
Crown levels	4	417.49	18.31**	114.14	2.79*
Dates	1	98.88	4.34*	247.25	6.05*
Trees x crown levels	8	77.71	3.41*	50.01	1.22
Trees x dates	2	11.98	0.53	21.96	0.54
Crown levels x dates	4	46.75	2.05	11.90	0.29
Trees x crown levels x dates	8	44.21	1.94	11.46	0.28
Error	30	22.80		40.85	

great. A comparison between the two methods for expressing foliage production is shown in Table VI. The coefficients of variation are high for both methods. However, adjustment for branch size reduced the coefficient by 66 and 47 per cent for Plots I and II, respectively. The amount of foliage per unit of "branch size" therefore promises to be a more satisfactory index for survey purposes than does the weight of foliage per branch.

TABLE VI — A Comparison Between Mean Weight of Foliage per Branch and Mean Weight per Unit of "Branch Size".

Plot	Weight of foliage per branch			Weight of foliage per unit of "branch size"		
	Standard deviation	Mean weight in grams	Coefficient of variation	Standard deviation	Mean weight in grams	Coefficient of variation
I	15.93	24.24	65.7%	4.77	21.34	22.4%
II	16.64	25.14	66.2%	6.39	18.32	34.9%

WEIGHT AND NUMBER OF SHOOTS

Estimates of the number of new shoots in relation to the amount of foliage per tree would provide data for evaluating their importance in limiting the size of the larch sawfly population. The ratio used here is the number of new shoots per 10 grams of estimated foliage weight. This value was calculated for each branch, and an analysis of variance conducted for each plot (Table VII).

TABLE VII — Analyses of Variance for Testing Tree, Crown Level, and Date of Sampling Effects and Their Interactions, Based on Number of New Shoots per 10 Grams of Estimated Foliage Weight.

Source	Degrees of freedom	Plot II		Plot I	
		Mean square	F	Mean square	F
Trees	2	177.13	7.87**	1343.94	20.77**
Crown levels	4	811.91	36.08**	338.60	5.23*
Dates	1	0.01	0.00	3.70	0.06
Trees x crown levels	8	31.99	1.42	43.16	0.67
Trees x dates	2	12.11	0.54	49.26	0.76
Crown levels x dates	4	60.90	2.71*	16.76	0.26
Trees x crown levels x dates	8	36.28	1.61	79.04	1.22
Error	30	22.50		64.70	

Tree differences are significant at the .01 level for both plots. Crown level differences are also significant at the .01 level for Plot I and at the .05 level for Plot II. The crown



level-by-date interaction may indicate that crown level differences did not follow the same trend for the early and late sampling periods, but it probably can be attributed to sampling variation. The number of new shoots per 10 grams of dry foliage weight for different portions of the crown are as follows:

Plot	Distances from top of tree in feet					
	0 - 5	5 - 10	10 - 15	15 - 20	20 - 25	25 - 30
I	—	21.5	13.7	8.3	3.0	1.4
II	23.6	17.0	19.0	13.1	9.8	—

These figures show that there is a decrease in the relative number of new shoots from the upper to the lower portions of the crown. The rate of utilization of new shoots for oviposition sites remains fairly constant throughout the crown. The higher concentration of shoots in the upper portions of the crown explains why this region is the first to show noticeable defoliation.

FOLIAGE WEIGHT AND SHOOT LENGTH

Both the weight of foliage per fascicle and the length of the new shoots may reflect the vigour of a tree. It is therefore possible that shoot length may provide a rough index of the amount of foliage. To test this hypothesis, the correlations between shoot length and weight of foliage in the basal fascicle were calculated for each tree. The correlations and degrees of freedom were as follows:

Tree	Plot I		Plot II	
	Correlation	Degrees of freedom	Correlation	Degrees of freedom
I	.489**	21	.787**	38
II	.170	24	.749**	52
III	.805*	12	.336	10

Three of these correlations are significant at the .01 level and one at the .05 level. This indicates that there is some relationship between shoot length and weight of foliage in the basal fascicle, but the agreement between the two variables is not consistent for all trees. The usefulness of shoot length as an indicator of foliage weight depends on the relationship between mean shoot length and mean weight of foliage per fascicle. The correlations between the branch section means for shoot length and foliage weight per fascicle were all quite low, and seem to indicate that even less relationship exists between the length of shoot and weight per fascicle for a section of a branch than between individual shoots and their basal fascicles. It must therefore be concluded that shoot lengths are of no practical value in estimating weight of foliage per fascicle.

NEEDLE LENGTH

Foliage weight is used in this paper as the basis for determining foliage variation. However, there is also considerable variation in needle length, and an examination of needle length may provide information on how the variation occurs. Needle length will therefore be discussed under the following headings: needle length and weight; and intra-fascicle variations in needle length.

NEEDLE LENGTH AND WEIGHT

The relationship between needle length and weight was tested by calculating the correlations between total needle length and oven-dry weight per fascicle for each group. The *r* values obtained were .967, .969, and .915 for Groups I, II, and III respectively, each with 28 degrees of freedom. These values are significant at the .01 level, indicating a linear relationship between needle length and weight of foliage. Most of the variation in foliage weight is therefore due to differences in the length of the needles. The regression coefficient, *b*, was similar for all groups, so the validity of using an average regression coefficient was tested by using the errors of estimate technique (Snedecor, 1946).

No significant differences were found between groups, and the use of an average regression coefficient is valid. The estimated weight of foliage in milligrams ( $Y$ ) based on total needle length per fascicle in millimetres ( $X$ ) is given by the formula  $Y = -2.988 + 0.04658 X$ .

### INTRA-FASCICLE VARIATION IN NEEDLE LENGTH

To obtain information on the intra-fascicle frequency distribution for needle lengths, the mean and variance were calculated for each fascicle. The correlations between these were .914, .941, and .959 for Groups I, II, and III respectively, showing that there is a strong linear relationship between the mean and variance.

The variability in fascicle length created difficulty in making direct inter-fascicle comparisons of the intra-fascicle frequency curves for needle lengths. However, an attempt was made to compare the shape of the curves for fascicles of different sizes by dividing each group of 30 into two size classes based on fascicle length (over 20 mm., and 20 mm. or less). The needle lengths for each fascicle were expressed as standard deviates and their frequencies tallied. There was some variation in the shape of the curves, but no consistent differences were evident either between groups or between size classes. The data were therefore pooled to give a larger sample. The observed frequencies and a free hand curve are shown in Fig. 1. The curve is bimodal, with a large peak occurring about one standard deviation to the right of the mean, and a smaller peak about one standard deviation to the left.

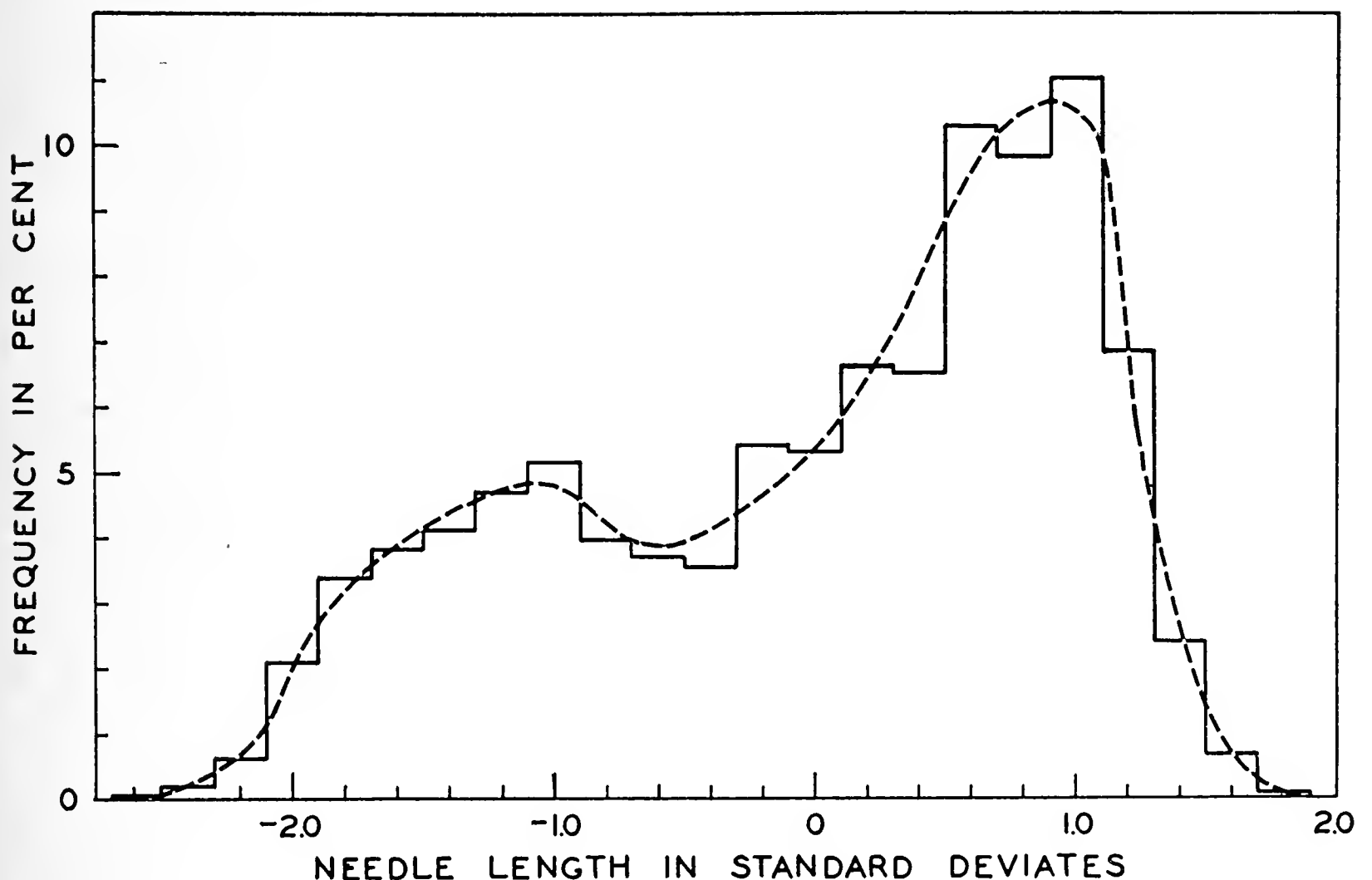


Fig. 1. Observed frequencies and a free hand curve of the frequency distribution of tamarack needle lengths expressed as standard deviates.

### DISCUSSION

Several different measures of foliage production on tamarack have been tested. The choice of a suitable measure will depend upon the objectives of the study and upon the resources in time and man-power.

Annual surveys are currently conducted to provide an index of larch sawfly abundance in different areas. These surveys indicate where outbreaks occur but do not show how the stands have been affected by sawfly attack. Surveys of tamarack foliage production in infested areas would furnish information that could be used to assess the degree of tree injury and to determine the interrelationships of the insect and its host in different types of stands.

The amount of foliage per unit of branch size is the most promising survey method that could easily be related to sawfly abundance. It seems impractical to sample the whole crown, and sampling would probably have to be confined to the mid-crown. Such sampling could provide data on the weight of foliage per branch or unit of branch size, and the number of new shoots per branch or unit of foliage weight. A second sampling on the same trees may be used to collect additional data on the number of eggs per unit of branch size and percentage of new shoots utilized for oviposition sites. To obtain the branch size, measurements equivalent to the width and length of the foliated portion of the branch should be taken, even if no foliage is present at the time of sampling. The above data would provide quantitative information on the following: (1) the relative foliage production per branch on different types of trees; (2) the trends in foliage production during the course of an outbreak; (3) the abundance of new shoots per branch in relation to the amount of foliage; (4) the number of eggs and weight of foliage per unit of branch size; and (5) the importance of the number of new shoots in limiting the size of the larch sawfly population. Evaluation of item (5) will require additional studies to be made on the oviposition behaviour of the larch sawfly since an apparent surplus of available oviposition sites may actually have a limiting effect on the size of the insect population. Both the searching ability of the insect and the suitability of available shoots will affect the number of shoots utilized for oviposition when shoots are scarce in relation to the number of sawfly adults. It is assumed that the female sawflies have sufficient searching ability to find any new shoots that have not already been used as oviposition sites. However, all of these shoots may not be suitable for oviposition at the time the insects are laying their eggs. It is possible that some shoots may not be sufficiently developed early in the season, while some may be too hard late in the season. If neither of these situations arise the percentage utilization is adequate and 100 per cent utilization would indicate that the number of shoots has probably had a limiting effect on the insect population.

Intensive studies on the foliage production of tamarack would be desirable in the development of life tables for the larch sawfly. This insect inhabits two universes at different stages in its life cycle, the tree and the forest floor. Therefore, it is desirable to express populations on an area basis, which would be applicable to all stages. The weight of foliage, number of new shoots, and number of shoots utilized for oviposition sites could be estimated on a tree basis, and then converted to an area basis. This would require branch counts in each crown level of the sample trees, and a count of the number of trees in different size classes in the sample plot. Foliage samples would have to be taken throughout the crown, since there are large differences in the amount of foliage per branch in the different crown levels.

If estimates of the production of foliage and shoots of tamarack, and of the abundance of adults, eggs, larvae, and cocoons of the larch sawfly are all expressed on an area basis, it would be possible to express any one of these quantities in terms of another. For instance, the number of mature larvae per unit of foliage weight would give the relative abundance of this stage of the insect for any type of stand, thus eliminating the difficulty encountered in comparing absolute sawfly populations on trees of different sizes. At the same time, absolute quantities would be available for following trends in tree characteristics or abundance of different stages of the insect for any particular stand.

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# New Termite-Repellent Wood Extractives

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## ABSTRACT

The researches of the analytical wood chemist should be synchronized with tests with wood-destroying fungi by the mycologist, and with living insects attacking wood by the entomologist. Proof cannot otherwise be obtained that the characteristic and unique extractive which he obtains from the wood of a tree reputed to be resistant to attack by fungi and insects is really the responsible chemical agent. Nymphs of the West Indian dry-wood termite, *Cryptotermes brevis* Walker, are especially desirable as experimental animals, besides being of ever-increasing economic importance in the tropics. Not only can they indicate the relative resistance of woods to termite attack, but they can also prove the value of the extractives obtained from the more desirable woods when such chemicals are used to impregnate least resistant woods.

Of the numerous extractives obtained by Prof. M. L. Wolfrom from Osage orange, they indicated the greater value of the unnamed substance I and tetrahydro-osajin, as compared with pomiferin, osajin, and other wood components.

Despite the stronger fungicidal action of pinosylvin recorded by Dr. Holger Erdtman of the extractives which he had obtained from Scots pine, they indicated that pinosylvin monomethyl ether is of much greater value in preventing insect attack at very great dilutions. Taxifolin from Douglas fir is of unexpectedly much greater repellency than numerous other extractives from other conifers.

The wood of the formerly neglected *Ryania speciosa* of Venezuela and Trinidad is unique in that five years after exposure to the air it is still immediately toxic to termites, and its extractive, a commercial insecticide, is not only toxic to them at great dilutions, but for seven years at impregnations of one-twentieth of one per cent continues to be repellent to *Cryptotermes brevis*.

Of the various new extractives obtained by Prof. F. E. King from the woods of African and South American trees reputed to be resistant to insect attack, only chlorophorin from the African iroko proves to have outstanding virtue as a preservative compound.

The natural resistance of any wood to fungi and wood-boring insects is due to some specific chemical constituent, usually present in comparatively small amount as compared with the lignin and cellulose which form the bulk of the timber. It must not be thought, however, that any minor constituent of a termite-resistant wood will prove to be the one specifically responsible for resistance to termite attack, no matter how characteristic it may be for a particular genus or species of wood. This has been discussed at length (Wolcott, 1948) and need not be further elaborated here. The present note is primarily to record the results of tests with extractives of woods recently obtained from Prof. F. E. King, formerly of Nottingham University, as well as a continuation of those previously reported (Wolcott, 1953), using the West Indian dry-wood termite, *Cryptotermes brevis* Walker, as the experimental animal.

Co-operation between chemist and biologist is most desirable from the very beginning of such an investigation, if the chemist is not to spend his time in working with the economically inessential constituents, rather than being able to concentrate his efforts on the one which is the major factor in determining the value of the wood. In the research being conducted by Dr. Conrado Asenjo of the School of Tropical Medicine in San Juan, on the wood of West Indian mahogany, *Swietenia mahagoni* Jacquin, each extractive fraction which he obtained from the wood with various solvents was tested as impregnations on the termite-susceptible wood flamboyán or Royal Poinciana, *Delonix regia* (Bojer) Raf. Those which did not repel the termite nymphs were immediately discarded, quite regardless of how interesting their constituents might prove from the strictly scientific standpoint.

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A tenth of the weight of finely comminuted chips of mahogany heartwood can be extracted with water, to obtain a dark-colored liquid containing the constituent responsible for the characteristic color of old mahogany. But flamboyán wood impregnated with this purplish water extractive is as readily eaten as untreated flamboyán samples. Moreover, the termites eating it temporarily have purple abdomens because of the ingested material which they have eaten. Obviously, this could not contain the constituent responsible for the resistance of mahogany heartwood to termite attack.

Midway in the progress of his investigations, Dr. Asenjo found that the waxy white substance which he had been extracting with ether petroleum from mahogany chips and which tests with termites indicated as being or containing the termite-repellent principle of mahogany, was no longer present in the most recently acquired material obtained from the local furniture manufacturers. Upon inquiry, they admitted that Santo Domingo as a source of timbers was no longer available, and instead they were using Honduras mahogany, *Swietenia macrophylla* King, from Mexico. From the standpoint of the cabinet-maker, this is an equally desirable wood, and the purchaser can be assured that it is a real mahogany. But as indicated by Wolcott (1950), the heartwood of Honduras mahogany has a termite-resistance rating no greater than the sapwood of the West Indian species, and it is hardly surprising that Dr. Asenjo could find in it little of the termite-repellent extractive characteristic of the local species. Visiting Haiti in person and there obtaining an ample supply of chips from the cabinet-makers using only the heartwood of *Swietenia mahagani*, he found the waxy white substance present in its accustomed amount. This incident is one indication of what had already been suspected from the widely differing termite-resistance ratings of woods of the same genus, or botanically of the same family. Consistently high ratings depend on the presence of a specific chemical constituent of each species of wood, which often is absent or present only in minimum amount in other species of the same genus, of a lower termite-resistance rating.

Of all the woods consistently found to be most resistant to dry-wood termite attack, the only one growing outside of tropical or sub-tropical regions is the Osage orange or bois d'arc, *Maclura (Toxylon) pomifera* (Raf.) Schneider, once widely used as a hedge fence in the Middle West and on the Great Plains before the invention of barbed wire. "It is considered the most durable of all North American timbers, and, inasmuch as the sapwood is very thin, even small-sized stems will give long service as stakes and posts" (Record and Hess, 1943). Its wood is even more termite-resistant than the heartwood of West Indian mahogany. Intrigued by its unique possibilities, Prof. M. L. Wolfrom of the Department of Chemistry of the University of Ohio commenced studies on its constituents. Of the preliminary samples submitted to entomologists of the University for testing as to toxicity, Mexican bean beetles found all non-toxic in the small amounts that could be extracted by Prof. Wolfrom. These frustrating tests were in reality entirely wrong in principle, for rarely are wood extractives toxic to insects, but merely repellent.

The substance which Prof. Wolfrom names Osajin showed little value in tests conducted in Puerto Rico in repelling the nymphs of *Cryptotermes brevis* on pieces of flamboyán wood impregnated with it at the maximum concentration which the limited amount of the sample made possible, for a minimum of 50 cc. of solution of the chemical is essential for complete submergence and impregnation of the standard experimental sample of flamboyán wood. The substance named Pomiferin, however, at 1% impregnation was repellent and protected flamboyán wood from attack for 880 days (Table I). Even more impressive is the record of tetrahydro-Osajin, which at 0.1% protected the flamboyán sample from being eaten for 707 days, and of another extractive which Prof. Wolfrom calls only "Substance I" of which the 0.1% impregnation was eaten only after 808 days. It must be kept in mind that these were only thin, surface impregnations on the very susceptible flamboyán wood, obtained by submergence in the solution of the chemical for ten minutes, purposely thus planned that comparable results might be obtained within a reasonable length of time with even the most repellent chemicals. For comparison with commercial chemicals, pentachlorophenol at 0.1% was eaten by termites in ten days, and only after 11 years at 1% did it cease to be effective in preventing the termites from tun-



neling into the test sample. The sample impregnated with 1% DDT was eaten in 37 days, but the 2% DDT impregnated sample has resisted termite attack for 12 years.

TABLE I. Days after Submergence for Ten Minutes in Solution before Attack by the West Indian Dry-Wood Termite, *Cryptotermes brevis* Walker.

tions of	0.01%	0.02%	0.05%	0.1%	0.2%	0.5%	1%	2%
achlorphenol (Monsato)				10	18	273	337*	
* slightly eaten in 337 days; not decisively tunneled for 11 years after impregnation								
T (commercial, 1944)			25	27	29	35	37	uneaten 12 years
in (Wolfrom)	51	53	55	58	61	END		
Osajin monomethyl ether	59	63	68	73	END			
iferin tri-methyl ether	98	101	109	110	112	END		
tance III (Wolfrom)	132	138	142	148	END			
Pomiferin dimethyl ether	154	155	156	225	END			
iferin (Wolfrom)	323	330	334	383	386	389	880	END
ahydro-Osajin	180	182	187	707	END			
tance I (Wolfrom)	130	226	236	807	END			
Maclura pomifera (Raf.) Schn.								
sylvin (Erdtman)	565	567	570	579	644	670	674	END
ydro Pinosylvin								
onomethyl ether	375	389	441	482	1278	1279	uneaten 5 years	
sylvin dimethyl ether	147	152	190	564	577	uneaten 4.5 years		
sylvin monomethyl ether	uneaten 5 years							
Pinus sylvestris L.								
ysin (Erdtman)	55	56	58	61	79	82	90	END
cembrin (Erdtman)	57	72	74	78	102	108	288	END
Pinus lambertiana Dougl.								
col (Erdtman)	1% eaten in less than a year							
tronellic acid (Erdtman)	473	475	477	479	493	503	561	END
Citronellidene acetic	16	24	469	470	478	496	568	END
id (Erdtman)								
folin (Erdtman)	150	154	1884	1887	uneaten in 5.5 years			
Pseudotsuga merrziesii (Mirb.)								
anco								
iodine (Merck)	84	204	sparingly in 7 years					
Ryania speciosa Vahl.								
oquinone (Eastman)	3	6	24	36	45	536	uneaten 11 years	
Tectona grandis L. f.								
rophorin (King)	73	137	138	147	234	uneaten in over 4 years		
Chlorophora excelsa								
enth. et Hook f.								
rosin (King)								
Zanthoxylum flavum Vahl.	5	7	11	13	16	57	60	END
omethyl Suberosin (King)	23	25	26	28	29	32	35	END
Chloroxylon swietenia DC.								
aretic acid (King)	4	6	16	20	22	53	83	END
Guaiacum officinale L.								
ene acetate (King)	4	6	11	16	19	26	END	
Vouacapoua americana Aubl.								
acapenol (King)	5	6	16	23	25	87	END	
Vouacapoua americana Aubl.								
ayl Vouacapenate (King)	13	14	16	23	33	77	END	
Vouacapoua americana Aubl.								
uic acid (King)	15	17	19	20	22	36	END	
Eberua falcata Aubl.								
eirin (King)	40	43	45	47	50	85	END	
Ferreira spectabilbis Fr. Allem.								
ysophanic acid anthrone (King)	62	70	79	82	87	96	END	
Ferreira spectabilbis Fr. Allem.								

Coniferous woods show great variabiliy in their resistance to the attack of the West Indian dry-wood termite, *Cryptotermes brevis* Walker, Sitka spruce, *Picea sitchensis* (Bong.) Carr., is among the most susceptible, while the West Indian pine, *Pinus occidentalis* Sw., almost equals the heartwood of mahogany in its resistance,

and the fine-grained, gummy heartwood of the bald cypress, *Taxodium distichum* (L.) Rich., from the swamps of the Gulf Coast States, is practically immune to attack. Dr. Holger Erdtman, of the Division of Organic Chemistry of the Royal Institute of Technology at Stockholm, Sweden, suggested that "pinosylvin might be the main cause of the well-known great durability of pine heartwood" (Erdtman, 1949). The sample of pinosylvin (3, 5-dihydroxystilbene), which he submitted for test, proved to confer long-continued resistance to termite attack at a dilution of 0.01%, but was eventually attacked after 565 days, and greater concentrations were subsequently eaten so that the 1% impregnation failed to protect flamboyán wood after 674 days.

Another constituent of pine extracted by Dr. Erdtman was pinosylvin monomethyl ether (3-hydroxy-5-methoxystilbene). "The ratio of pinosylvin monomethyl ether appears to be rather constant in Scots pine (*Pinus sylvestris*) usually being between 1:3 and 1:4. Pinosylvin, as a rule, is a stronger fungicide than its monomethyl ether." The impregnation of 0.01% of pinosylvin monomethyl ether on flamboyán wood, using the same technique as with pinosylvin, is still immune to attack by dry-wood termites five years later, although they have stained it with deposits of liquid excrement in mute indication of an otherwise susceptible wood that they cannot eat. If the pinosylvin constituent of pine is the stronger fungicide, it is apparent that its monomethyl ether is very much more permanently repellent to dry-wood termites.

The contrast in permanence of resistance is possibly greatest between pinosylvin and its monomethyl ether, but dihydropinosylvin monomethyl ether at 0.01% repelled termite attack for over a year, and the sample impregnated with 0.5% was not eaten until four and a half years after impregnation. The sample of pinosylvin dimethyl ether was not received until later, thus the record is for a shorter time, but the impregnation at 0.5% has not yet been attacked after over four years' exposure.

Erdtman noted that the repellent constituents of Scots pine are more abundant in the periferal area of the heartwood than in its central portion. The nymphs of *Cryptotermes brevis* appear to be in entire agreement with him, attacking first the central heartwood samples cut from an entire timber of *Pinus sylvestris* L. which he sent from Sweden, and not the periferal heartwood samples until forced to do so by lack of others which they could eat.

In tests with other species of wood, even the peripheral heartwood of *Pinus sylvestris* is not very resistant to dry-wood termite attack, but is more so than sugar pine, *Pinus lambertiana* Dougl., of which such constituents as Chrysin (5, 7-dihydroxyflavone) and Pinocembrin (5, 7-dihydroxyflavonone) made samples of flamboyán at 1% impregnations resistant only for 90 and 288 days respectively. Cedrol (Erdtman) at impregnations of 1% fails to protect flamboyán wood for as much as a year. This is hardly surprising, as the lighter-colored cedar sapwood of commercial cedar chests is often eaten by dry-wood termites in the tropics, and even the heartwood is but moderately resistant to their attack.

Australian cypress pine, *Callitris glauca* R. Brown, has an odor most repulsive to man, and when freshly cut is entirely immune to attack not only by termites but even by marine borers, as is recorded by Edmondson (1955). Exposed to the air, this wood eventually becomes somewhat more susceptible, but is still very resistant to termites. Callitrol from the wood itself not being available, Erdtman sent plus-Citronellidene acetic acid and d-Citronellic acid, which is its synthetic analogue, both of which proved to have almost the same permanence of resistance: at 1%, being eaten in 561 and 568 days.

Taxifolin (3, 5, 7, 3', 4' -pentahydroxyflavonone), a constituent of Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco (= *P. taxifolia*), still protects the flamboyán sample from termite attack five years after impregnation with 0.2%. It may be presumed that only a very small amount of taxifolin is present in Douglas fir, for this wood is little more resistant than that of most pines and cedars, and is commonly subject to attack as plywood in the tropics.

The first insect-repellent chemical to be extracted from a wood of long-proven durability is beta-methylanthraquinone or "Tectoquinone" from East Indian teak, *Tectona grandis* L.f., now commercially available as a synthetic product as well

as extracted from the wood itself. The sample of flamboyán wood impregnated with 1% tectoquinone has successfully resisted termite attack for nearly eleven years, but the fact that lesser concentrations were eaten in a comparatively short time raises the question whether it is really the most termite-repellent constituent of teak. Certainly as compared with pinosylvín monomethyl ether, it is not nearly as effective, and a new generation of chemists might discover some much more powerful termite-repellent present in smaller amount.

Of the newer extractives, none is so interesting as Ryanodine, obtained from the wood of *Ryania speciosa* Vahl., of Trinidad and Venezuela. In Trinidad, farmers used to be advised to clear their pastures of the bushes of "Bois L'agli", much as one would try to eliminate guava bushes in Puerto Rico, or thickets of blackberries, or hawthorn in New England, but by now the commercial value of these once proscribed bushes is so great that official regulations prevent their being offered for sale with trunks of less than a certain diameter. The insecticide first developed by Merck, and later taken over by S. B. Penick & Co., has exceptional value against certain insects. Even five years after cutting and exposure to air, a single piece of ryania wood in a petri dish, with seven or eight pieces of equal size of other woods present, within 24 hours kills all the termites present, huddled as far away as possible from the toxic wood. Pests of books in mahogany bookcases with tightly-closed glass doors disappear when lengths of ryania wood are enclosed with them: truly a wonderful boon to housekeepers in the tropics. Impregnations at least concentrations on flamboyán wood are toxic at first, and nearly seven years later that at 0.05%, while no longer toxic, is still sparingly eaten.

Prof. F. E. King of Nottingham University in England, now with British Celanese Limited, has been working for a number of years on the constituents of woods, and through the good offices of Dr. Erdtman, a sample of his Chlorophorin was made available for testing with *Cryptotermes brevis*. Chlorophorin, a modified pinosylvín with a long chain attached, obtained from the African tree Iroko, *Chlorophora excelsa* Benth. & Hook f., is a dull greenish powder readily soluble in acetone of which impregnations were made on standard samples of flamboyán wood. That treated with 0.2% was eaten in 234 days, but that treated with 0.5% is still uneaten after four and a half years.

Prof. King subsequently sent samples of nine other extractives which he had obtained from various tropical trees. In some of these, at the maximum concentration of impregnation permitted by the limited supply of extractive, tests were completed so quickly as to leave in doubt whether these were in reality the extractives which might be responsible for the termite-resistance of the trees from which they had been taken. It is of course possible that the impregnations at 1%, which were eaten so promptly, might parallel in character those of DDT, which at 2% is apparently permanently immune to termite attack, despite the fact that its 1% impregnation was so promptly attacked. Certainly none of the nine extractives not even the very difficult to dissolve chrysophanic acid anthrone, is as permanently repellent at any dilution as was chlorophorin.

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# Soil Poisons for the Prevention and Control of Subterranean Termites in Buildings

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## ABSTRACT

*Subterranean termites are among the primary insect enemies of wood and cellulose products. Good construction practices will reduce the incidence of termite attack substantially, but builders often do not give enough attention to preventive measures. Therefore, in locations where these insects are abundant, it is advisable to provide protection by using chemicals to poison the soil.*

*During recent years, the Forest Insect Laboratory at Gulfport, Mississippi, has established comparative tests in Mississippi and the Panama Canal Zone to determine the effectiveness of numerous chemicals used as soil poisons. Field tests were designed to: (1) determine the value of poisoning the soil prior to pouring concrete slabs in building construction; and (2) simulate in certain respects trench treatment along the foundations of buildings. The most promising formulations were applied experimentally to infested buildings. These experiments demonstrate that certain of the chlorinated hydrocarbons give a longer period of protection against subterranean termites than most of the chemicals formerly used for this purpose. The results of these tests and the practical application of the insecticides are presented in this paper.*

## INTRODUCTION

Subterranean termites are widely distributed over the tropical and temperate parts of the world, and they seem to be extending their range northward.

The key to termite control lies in construction which prevents or discourages attack. The fundamental principle is to prevent them from establishing or maintaining their contact between the soil, from which they obtain moisture, and the woodwork of buildings, on which they feed. This could be accomplished, to a great extent, if architects, contractors, and home builders would give more consideration to the problem.

Termite activity can be discouraged by removing stumps, roots, and debris from the site and by grading to keep the site dry. Adequate clearance between the soil and woodwork, as well as proper ventilation, should be provided for buildings having crawl space. Foundations should be impervious to termites—solid concrete is preferable. Hollow block or tile foundations should be capped with 4 inches of reinforced concrete or provided with good termite shields. Expansion joint fillers resistant to termite penetration should be used in slab-on-ground construction. Pressure-treated wood for sills, plates, and headers may be desirable where the hazard is extreme.

No matter how carefully constructed, however, any untreated wooden building within the range of termites is vulnerable to their attack. In regions where termites are abundant, poisoning the soil with chemicals is advisable to provide additional protection. The poisons are used as a supplement to good construction—not as a substitute for it. Chemical treatment of soil before pouring concrete slab floors is particularly valuable. Most of the cost of treating soil, either as a preventive or remedial measure, is the labor for application. Long-lasting chemicals are needed to reduce frequency of re-treating.

Soil poisons have been used in the United States for many years, but those generally recommended had various limitations. During recent years the United States Department of Agriculture has intensified the search for better poisons. Most of the research is conducted by the Forest Insect Laboratory, Gulfport, Mississippi. The Laboratory has extensive field installations near Gulfport, and lesser ones in other parts of the United States and in the Panama Canal Zone.

This article points out the best formulations found to date and discusses briefly their practical application. It should be remembered that the tests are still in progress

<sup>1</sup>Acknowledgment is gratefully made to H. C. Secrest and R. C. Morris, entomologists formerly connected with this Laboratory, who established many of the tests and collected much of the data in these studies.



and that higher concentrations and dosages are being added to the tests with the view of extending the period of protection. The list of formulations suggested for use may be altered upon completion of the work.

### TEST METHODS

The first field tests reported herein were installed during 1944 on the Harrison Experimental Forest, about 20 miles north of Gulfport. These tests were expanded in 1946, and at the same time a series was established in the Panama Canal Zone. Many new insecticides have been added since 1946. The Mississippi tests are located in a pine-hardwood forest in a light, sandy loam soil with a clay subsoil. The Canal Zone tests are in a jungle area having a heavy type of soil.

Several of the most promising formulations are being tried also under practical conditions in buildings damaged by termites. These practical applications were established during the period 1944 to 1952. They are in North Carolina in sandy soil.

Three methods of testing are used.

*Ground-board tests* are intended to determine the most effective formulations and dosages for poisoning the soil prior to pouring concrete slabs. All vegetation is removed from a 17-inch square of soil, then the chemical is sprinkled evenly over the soil surface at the desired rate of application. After the chemical has soaked into the soil, an untreated sapwood pine board measuring 1 by 6 by 6 inches is laid flat on top of the ground in the center of the treated area, so that termites must cross or penetrate the treated soil before they can attack the board.

*Stake tests* are designed to simulate in certain respects the trench application of soil poisons around the foundations of buildings. Two cubic feet of soil are removed to make a hole 15 inches in diameter and 19 inches deep. After the soil is treated with the desired dosage of chemical and replaced in the hole, a 2-by 4-by 18-inch untreated sapwood pine stake is driven to a depth of 12 inches in the center of the treated soil.

In both the ground-board and the stake tests, ten replicates of each treatment are used in a randomized block design. Treatments are considered to have failed when termites penetrate the treated soil and attack the wood. When 50 per cent of the stakes or boards of a treatment are attacked, the test is closed.

*Building tests* are treatments of buildings that have become infested with termites. The chemicals are applied in shallow trenches along the inside and outside of concrete or brick foundations. Most buildings have two or three porches and at least one room with crawl space underneath. Each porch or room is considered as a test unit for inside treatments—i.e., those underneath the house and thus partially protected from the weather. The outside treatments are largely around basement entrances, each entrance being regarded as a test unit. When termites penetrate the treated soil and construct tubes on the foundation, the treatment is considered to have failed.

### RESULTS

The field installations, being fully exposed to the weather, are more severe trials than the building tests. In general, the formulations and dosages that are effective in either the ground-board or stake tests can be relied upon to give a high degree of protection to buildings. Several formulations that gave poor results in the field tests offered good protection underneath buildings.

Main results are summarized in Tables I, II, and III. In evaluating these data, it is considered that only formulations giving good results for at least 5 years in one or both types of field tests in Mississippi can be safely recommended for use in the United States. The following formulations are among the best tested thus far, and are suggested for practical use to protect buildings:

1. Benzene hexachloride, 0.8 per cent gamma in No. 2 fuel or water emulsion.
2. Chlordane, 1.0 per cent in No. 2 fuel or water emulsion.
3. Dieldrin, 0.5 per cent in No. 2 fuel oil or water emulsion.
4. DDT, 8.0 per cent in No. 2 fuel oil.
5. Trichlorobenzene, 25.0 per cent (by volume) in No. 2 fuel oil.
6. Sodium arsenite, 10.0 per cent in water.

TABLE I — Effectiveness of Soil Poisons in Ground-board Tests in Mississippi and the Panama Canal Zone.

FORMULATION (percentages by weight)	Location of test	Year estab- lished	Dosage per square ft.	Proportion of ground-boards undamaged by termites after exposure for									
				1	2	3	4	5	6	7	8	9	10
				yr.	yrs.	yrs.	yrs.	yrs.	yrs.	yrs.	yrs.	yrs.	yrs.
				Percentage									
				Pints									
Benzene hexachloride In No. 2 fuel oil 0.4 per cent gamma	Miss.	1948	1/2	100	100	100	100	90	50				
	Miss.	1948	1	100	100	100	100	100	100	90			
	C. Z.	1951	1	100	70	50							
			2	90	90	60	40						
0.5 per cent gamma			1	100	100	100	100	100	100	100	90		
0.8 per cent gamma	Miss.	1948	1	100	100	100	100	100	100	100	90		
In water emulsion 0.4 per cent gamma	Miss.	1948	1/2	100	100	80	70	70	60	60	60		
	Miss.	1948	1	100	100	100	100	100	100	80	80		
	C. Z.	1951	3	90	90	80	50						
	Miss.	1948	1	100	100	100	100	100	100	100	100		
0.8 per cent gamma				100	100	100	100	100	100	100	100		
Chlordane In No. 2 fuel oil 1.0 per cent	Miss.	1948	1/2	100	100	100	100	100	100	100	100		
	Miss.	1948	1	100	100	100	100	100	100	100	100		
	Miss.	1948	1/2	100	100	100	100	100	100	100	100		
	Miss.	1948	1	100	100	100	100	100	100	100	100		
In water emulsion 2.0 per cent	C. Z.	1951	2	100	90	90							
In water emulsion 2.0 per cent	Miss.	1948	1/2	100	100	100	100	100	100	100	100		
	Miss.	1948	1	100	100	100	100	100	100	100	100		
	C. Z.	1951	2	100	70	50	30						
	C. Z.	1951	3	100	100	70	70						
DDT In No. 2 fuel oil 5.00 per cent	Miss.	1946	1/2	100	100	100	70	50					
	Miss.	1946	1	100	100	100	100	80	80	80	80	80	80
	C. Z.	1951	1	90	80	60	50						
	C. Z.	1951	2	100	90	70	50						









TABLE III — Effectiveness of Soil Poisons in Controlling Termites in Buildings During 10 Years of Service.

FORMULATION	Dosage per 10 lineal ft.	Underneath buildings				Outside of buildings				Total	
		Units treated		Undamaged		Units treated		Undamaged		Units treated	
		Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage
Coal tar creosote In No. 2 fuel oil 50.0 per cent	2	19	95	8	63	27	.85				
Chlorinated toluene (2-chloro-6-nitro-toluene) In No. 2 fuel oil 25.0 per cent	2	23	100	8	50	31	87				
DDT In No. 2 fuel oil 5.0 per cent 10.0 per cent	4 4	59 22	97 100	28 7	75 57	87 29	90 90				
In water emulsion 5.0 per cent	4	39	97	4	50	43	93				
Orthodichlorobenzene In No. 2 fuel oil 25.0 per cent	2 4	86 6	92 100	19 2	42 50	105 8	83 75				
Pentachlorophenol In No. 2 fuel oil 5.0 per cent	4	17	94	3	33	20	75				
Sodium arsenite In water 10 per cent	2	39	100	0	—	39	100				

A dosage of one to one and one-half gallons of any one of the emulsions or the water solution of sodium arsenite per ten square feet of surface area is recommended for over-all treatment before pouring concrete slabs, the dosage depending on the type of fill material. Four gallons per ten cubic feet of soil should be used for treating around foundations.

These concentrations and dosages provide a good margin of safety, so that a long period of protection can be expected. Since the cost of the chemical usually is only a small portion of the total cost of treating a building, it appears logical to use enough chemical to prevent attack for as long as possible.

The data in Tables I and II show that much heavier dosages and concentrations are necessary in the Canal Zone than in Mississippi. For example, 2 per cent chlordane in water emulsion at a dosage of one pint per square foot in ground-board tests in Mississippi is still 100-per cent effective after seven years; in the Canal Zone, a dosage of two pints per square foot was only 30-per cent effective for four years.

Chemicals that gave 50-per cent or less protection for five years (when tested at practical concentrations and rates of application) are considered inferior to those suggested for use. These include acetylene tetrachloride, chlorinated nitrotoluene, copper ammonium fluoride, copper naphthenate, copper sulphate, coal-tar creosote, coal-tar creosote plus orthodichlorobenzene, hexachloroethane, lead arsenate, methoxy-chlor, monochloronaphthalene, orthodichlorobenzene, pentachlorophenol, sodium dinitroorthocresolate, and zanthane.

### PRACTICAL APPLICATION OF SOIL POISONS

As indicated before, soil poisons have found very wide use in the United States for the control of active infestations of subterranean termites in buildings. As supplements to good construction, they are practical and effective in preventing attack in new buildings. Since there are so many variations in construction, a detailed discussion of preventive and remedial treatments is impossible. Essentially, treatment involves the application of the insecticide in such a way that it forms a barrier to termite entry.

**PREVENTIVE MEASURES:** Slab-on-ground construction is very susceptible to termite attack, and remedial measures are difficult and expensive; therefore, prevention is highly desirable. Protection can be secured for many years by poisoning the soil, before the slab is poured, with any one of the previously listed emulsions or a water solution of sodium arsenite.

Treatment should be made after all filling and grading is complete. Critical areas, such as along foundation walls and around plumbing, should be treated by the trenching method described later under remedial measures at the rate of 4 gallons per 10 linear feet of trench. In addition, an over-all surface treatment at a dosage of not less than 1 gallon per 10 square feet is recommended if the fill is soil or unwashed gravel. If cinders, washed gravel, or similar coarse material is used in the fill, the dosage should be increased by at least one-half. Voids in hollow-block foundations should be treated with a dosage of at least 2 gallons per 10 linear feet of wall. For buildings having crawl space or basements, the trench and void treatments can be used as preventive measures without an over-all surface application.

**REMEDIAL MEASURES:** In remedial treatment, slab-on-ground construction presents the most serious problems, because it is difficult to get the poisons where they will be effective. One method of treating is to drill holes through the concrete slab at any point where termites may enter. The holes should be spaced about a foot apart to ensure proper treatment of the soil underneath. Another method is to drill through the foundation walls from the outside and force the chemical just underneath the slab along the inside of the foundation and along expansion joints. Any one of the formulations listed above should be applied at the rate of 4 gallons per 10 linear feet of foundation or expansion joint.

To treat buildings having crawl space or basements, dig a trench adjacent to and around all piers and pipes and along the sides of foundation walls. A trench 6 to 8 inches deep and about the same width is ample for solid concrete foundations that

have not developed cracks. While the trench is open, one of the previously mentioned formulations should be poured in at a rate of 2 gallons per 10 linear feet of trench. Then, as the excavated soil is put back into the trench, it also should be treated at the rate of 2 gallons per 10 linear feet. This rate of application is equal to about 4 gallons per 10 cubic feet of soil, assuming that the chemical spreads downward and outward from the trench. For brick, hollow block, and concrete foundations that have cracked, care should be taken to dig the trench to the footing. This is a precaution to prevent termites from gaining hidden entry through voids in these types of foundations. The amount of chemical applied in deep trenches should be increased correspondingly. Voids in hollow block foundations should be treated as described under preventive measures.

**WARNING!** *All of these chemicals are poisonous if taken internally, and some of them can be absorbed through the skin. If they are spilled on the body, they should be washed off immediately with warm, soapy water. Sodium arsenite is very toxic to plants and should not be used where the roots of valuable plants will contact it. The oil solutions will damage plants if applied to their roots.*

### DISCUSSION

E. B. WATSON. What are the insecticides most commonly used by commercial pest control operators against subterranean termites at the present time?

H. R. JOHNSTON. Chlordane probably is more widely used than any other insecticide by commercial operators. DDT, BHC, dieldrin, sodium arsenite, and others are also used.



# Insect Vectors of the Dutch Elm Disease in the Province of Quebec

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## RÉSUMÉ

L'urgence de l'étude approfondie des mœurs des divers insectes qui fréquentent l'orme ou s'y reproduisent s'est fait particulièrement sentir dans la province de Québec au moment où la présence du *Ceratostomella ulmi*, l'agent causatif de la maladie des ormes, fut définitivement établie, à l'automne de 1944.

On crut d'abord que le Scolyte indigène de l'orme *Hylurgopinus rufipes* (Eich.) pouvait être responsable de ce transfert étant donné l'absence du *Scolytus multistriatus* (Marsham), principal vecteur de cette maladie aux Etats-Unis et en Europe. Toutefois les expériences entreprises pour vérifier le bien-fondé de cette hypothèse furent peu concluantes.

L'étude bio-écologique des charançons de l'orme (*Magdalis barbata* Say, *M. armicollis* Say, *M. inconspicua* Horn) retint notre attention dès le printemps 1946. Les charançons adultes passent d'abord par une phase alimentaire sur le feuillage des ormes en mai et début de juin. Au moment de la reproduction, dix jours environ après leurs métamorphoses, ces insectes s'attaquent surtout aux écorces, font de multiples enfoncements principalement à l'aisselle des rameaux. Les expériences entreprises en 1947 pour démontrer la possibilité du transfert de la maladie par ce dernier genre d'activités des charançons furent couronnées de succès.

Les observations sur le terrain et la répétition des expériences durant cinq années consécutives permirent de nous assurer du rôle néfaste que jouent ces insectes, en particulier *M. barbata* et *M. armicollis*, dans la propagation de la maladie des ormes. Ces travaux ont été exécutés à Berthierville au laboratoire du Ministère des Terres et Forêts de Québec, sous la direction du Docteur Lionel Daviault.

Our most recent extensive studies of most insects of the elm tree go back especially to between 1946 and 1951. Our summer laboratory was at Berthierville and Dr. L. Daviault was in charge.

As it is impossible in a few lines to summarize all the work done in this period, we must pass over the life cycle study made on the native elm bark beetle, *Hylurgopinus rufipes* (Eich.), which is the sole Scolytid living in elms in Quebec. Much attention was paid to the snout beetles and their parasites. The life cycle of hosts and parasites had been studied previously to, or was conducted simultaneously with, the experimental work on the possible vectors of the disease.

In Quebec three different species of snout beetles live on elm trees; these are *Magdalis barbata* Say, *M. armicollis* Say and *M. inconspicua* Horn. The last one is not common but is found in several places in the St. Lawrence valley; the other two are widely scattered and generally are represented in very large numbers.

The life cycle of the three snout beetles is a one year period, from May to May or June to June except for a small percentage of slow growing larvae. The earliest of the three is *M. barbata*, followed 15 to 20 days later by the other species. So, generally by the end of June, the three species are in flight, but the first one more numerous than the other two. Later on, just the reverse is the situation. *M. armicollis* and *M. inconspicua* are seen more often than *M. barbata*.

In order to collect a large number of weevils of various species to be used in our experiments, branches of elm trees infested with larvae and pupae were collected in the field during the first week of May, and placed in appropriate containers in the laboratory for recovery of the adults. As soon as the adults emerged from the wood, they were transferred to cages containing elm foliage, on which they feed readily. As a matter of fact, newly formed adults of these insects are very fond of new leaves, which they devour all day long. Some adults were kept in small glass jars covered with wire-screen



into which fresh leaves were placed every other day; others were reared directly on foliage enclosed in large cages.

The feeding on elm foliage lasts about twenty days, and then, the mating takes place which, incidentally, is very peculiar in that long and various ceremonies happen before the female accepts coition. After this period, the females are attracted by elm wood, and they can be seen chewing elm tree bark either at a branch node or in the natural cavities of the bark, in order to obtain food, and also to lay their eggs in the inner bark. The numerous holes dug by the females at this stage of their life reach only the inner bark when the bark is thick; in smaller limbs they reach the interior layers of the inner bark and very often the cambial zone, or even the wood itself, especially in the small branches of the crown. The diagrams A and B in Fig. 1, illustrate this peculiar behaviour of the female weevils.

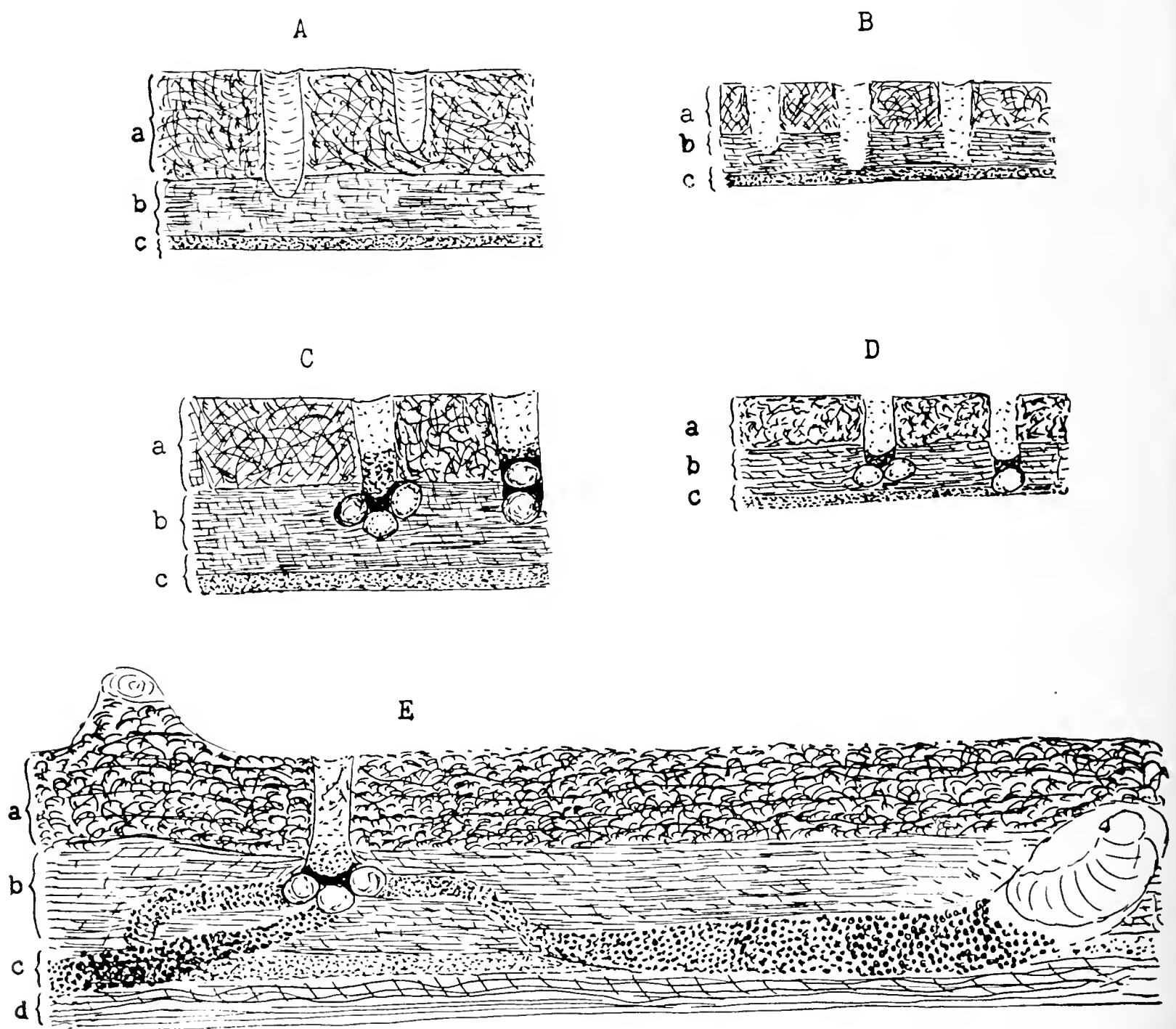


Fig. 1. Details of weevil borings and larval mines in elm bark; A, Borings in thick bark only reaching the phloem; B, Borings in thin bark sometimes reaching the cambium; C, Borings showing the location of weevil eggs in thick bark; D, Borings showing the location of weevil eggs in thin bark; E, The typical course of a larval mine during the summer months. a, Cortex layer; b, Phloem layer; c, Cambium layer; d, Xylem.

It has been noticed that, under natural conditions, female weevils dig some of these cavities in different branches of the same tree, or in adjoining elms. Occasionally the female leaves a contaminated elm to go to a healthy one, and it can be assumed that this contributes to the dissemination of the disease. In order to prove this point, a series of experiments and observations were undertaken.

The experiments were carried out with the two most common species of elm weevils, that is *Magdalis barbata* and *M. armicollis*; the third species, *M. inconspicua*, could not be found in sufficient numbers.

In a first series of experiments, weevils which had been fed for 10 to 20 days on leaves were artificially infested on their beak with vegetative elements or spores of the fungus, *Ceratostomella ulmi*, and later they were confined in appropriate cages around branches or trunks of sound elm trees.

The cages used in these experiments were about ten inches long, and wide enough to allow free circulation of adult weevils over the twigs or the trunk of the trees. The cages were held in place by a string at top and bottom; an opening on the side, closed with a zipper, allowed observations at all times. These cages proved very convenient, and prevented escape of the insects.

To further incite the females to feed on the bark, all the leaves were removed from the portion of the twigs inclosed in cages. The females thus confined, either alone or in company of a male, started at once to dig into the bark. Examination of the twigs the following days always revealed several cavities in the cracks of the bark. The insects can live several days even without any foliage, and they are very active, drilling numerous holes through the bark. When groups of ten individuals are confined in a same cage, it is not unusual to trace between 50 to 100 holes dug by the weevils during the first three or four days of their captivity.

The numerous contacts with the inner bark, especially during the first days of their captivity, when the insects are carrying fresh fungus material, permit the introduction of the disease. External manifestation of the disease, however, requires from three to five weeks; the first symptoms of the disease are noticed on the top leaves, which turn yellow or curl up, and finally fall. The subjacent wood also appears marked with brownish streaks.

Our experiments were carried out at different periods of the season, in order to find out at which time the elms were most susceptible to infection. On the other hand, the work depended to a great extent upon the possibility of obtaining adults. They are quite abundant in May and the beginning of June, but later on in the season they are scarce. Results obtained in these various experiments are summed up in Table I.

TABLE I — Results of Experiments on the Transmission of *Ceratostomella ulmi* by the Elm Weevils in 1951.

Date when experiments started	Species	Number of elms subjected to experiments	Number of elms infected	% of infection
June 10	<i>Magdalis barbata</i>	10	4	40
June 17	<i>Magdalis barbata</i>	20	3	15
June 22	<i>Magdalis barbata</i>	10	3	30
June 25	<i>Magdalis armicollis</i>	4	1	25
July 4	<i>Magdalis barbata</i>	20	2	10
July 9	<i>Magdalis armicollis</i>	10	—	—
July 11	<i>Magdalis barbata</i>	10	1	10
July 13	<i>Magdalis armicollis</i>	6	—	—
July 13	<i>Magdalis barbata</i>	4	—	—
July 16	<i>Magdalis armicollis</i>	4	—	—

In another series of experiments, the procedure was different. The weevils were confined with elm foliage for about twenty days and, after this period, which is sufficiently long to permit maturation and mating, the females were given elm branches already contaminated by *Ceratostomella ulmi*, on which to deposit their eggs. By watching for the moment when they completed the digging of a hole in the bark, they were transferred to sound trees in the same type of cages as for the weevils artificially infected with *C. ulmi*. These female weevils dug new holes in the sound tree and after that deposited their eggs. As can be seen, these insects behaved under the conditions of our experiments exactly as they would have in nature. The important question was, however, whether or not the insects could transmit the disease in these artificial conditions. This type of experiment also proved successful. Two elms out of ten presented all the symptoms of the disease.

In all these experimental cases, the disease was first detected by the observation of the ordinary symptoms: wilting and drooping of the leaves, and the presence of brownish streaks in the wood. It was further checked by the culture of parcels of wood on Sabouraud agar medium. This fungus is easily identified by the way it develops in concentric zones, and also by the formation of quite characteristic synnema.

Both series of experiments carried out during 1951 tend to prove without any doubt that weevils under the particular conditions prevalent in our country are capable of transmitting the Dutch elm disease. In fact, individuals artificially infected with the pathogen can during the course of their natural activities introduce the fungus into the deep layers of the bark where it can spread throughout the tree. Furthermore, according to their natural habits, these insects are also apt to become contaminated and thereafter introduce the infestive germs.

### DISCUSSION

C. M. BAETA NEVES. Je vous prie d'avoir la gentillesse de m'informer si l'attaque insectes vecteurs de la maladie des ormes dans la Province de Québec, est précédée, comme au Portugal, de quelques saisons d'affaiblissement des arbres, et spécialement d'une défoliation par d'autres insectes.

A. ROBERT. Les charançons, il est vrai, se nourrissent sur le feuillage avant de déposer leurs oeufs sur les fines branches du sommet, mais leurs dégâts sont, en général, peu considérables, et on ne peut vraiment pas attribuer l'attaque à une si légère défoliation. D'autre part, les charançons perforent l'écorce en divers points avant de pondre leurs oeufs. Les premières perforations contribuent certainement à assécher les couches profondes de l'écorce et à créer ainsi un milieu plus favorable à la réception des oeufs.

# Les Ennemis naturels de l'*Ennomos quercinaria* (Hfn.) lors de sa récente pullulation en Sarre

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## RÉSUMÉ

Au cours d'une invasion massive en Sarre, sur hêtres et charmes, de 1952 à 1954, nous avons étudié les parasites de la géométride *Ennomos quercinaria* (Hfn.) et sa disparition due à une polyédrose. Le rôle des oiseaux dans la destruction des chrysalides a été observé. Parmi les parasites nous citerons en premier lieu les hyménoptères classés en 3 catégories: (a) ceux qui s'attaquent aux oeufs comme par exemple le proctotrupide *Aholcus dalmanni* (Ratz.); (b) ceux qui s'attaquent aux chenilles tel *Eulimneria* (Ichneumonide) ou *Macrocentrus abdominalis* (F.); (c) ceux qui s'attaquent aux chrysalides tels les *Pimpla* *P. instigator* (F.) et *P. rufata* (Gm.) et le *Lissonota buoliana* (Hart.). Viennent ensuite les diptères tachinidés; l'espèce la plus fréquente est *Ctenophorocera pavidus* (Meig.); puis nous citerons *Blondelia nigripes* (Fal.) et deux espèces du genre *Phryxe*; *P. nemea* (Meig.), *P. longicauda* (Wainw.). En 1954 une maladie à virus apparaît décimant les chenilles. Celle-ci est immédiatement pressentie d'après l'aspect des arpenteuses, lesquelles pendent le corps flasque ou plus ou moins desséché, accrochées à leur fils, puis vérifiée au laboratoire par des frottis qui révèlent la présence des corpuscules subpolyédriques caractéristiques. Le virus déterminant cette polyédrose rentre dans le genre *Borrelina* et en raison de sa localisation géographique nous l'avons nommé *Borrelina* (Bollea) *saraviensis*. L'année suivante (1955) de nombreuses recherches ne permirent de récolter que six chenilles; trois d'entre elles étant atteintes de polyédrose et une parasitée par la tachinide *Ctenophorocera pavidus*. En 1956 aucune chenille d'*Ennomos* n'a été rencontrée. Cet exemple de l'invasion des chenilles dévastatrices de feuillus d'*Ennomos quercinaria* anéantie après trois ans de gradation par une maladie à polyèdres vient s'ajouter aux exemples de viroses déjà connues et souligne leur importance décisive pour le rétablissement d'un équilibre biologique momentanément rompu par la pullulation d'un ravageur, équilibre que la multiplication intensive naturelle des insectes parasites n'arrivait pas à rétablir.

Les chenilles arpenteuses de la géométride *Ennomos quercinaria* (Hfn.) ont pendant trois années consécutives (1952-54) dévasté les forêts de feuillus situées immédiatement au nord de la ville de Sarrebruck, amenant des défoliations totales de charmes et de hêtres.

Une telle abondance d'*Ennomos* n'avait jusqu'à présent été constatée qu'une fois en Europe en 1917 (Krausse, 1919) et, chose curieuse, en Sarre dans le même district forestier de Fischbach, d'où l'intérêt tout particulier présenté par les ravages observés en ces dernières années.

Une autre espèce *Ennomos subsignaria* (Hbn.) est connue depuis longtemps en Amérique du Nord par les diverses attaques qu'elle a faites à plusieurs reprises dans les forêts de divers états du Centre et de l'Est des Etats-Unis et au Canada (Broadwell, 1880, 1908, 1909). Il est par ailleurs intéressant de remarquer que les cycles biologiques de ces deux papillons sont tout à fait comparables.

De la rareté des pullulements d'*Ennomos quercinaria* il résulte que personne n'avait pu apporter jusqu'à ce jour de précisions sur les ennemis naturels de cette espèce. Comme nous avons pu suivre de très près la dernière invasion dans les forêts sarroises il nous a été possible d'étudier les facteurs intervenant dans la limitation ou dans la destruction naturelle de ces chenilles arpenteuses puisque non seulement nous avons pu assister à la multiplication massive des insectes parasites habituels mais encore nous avons vu apparaître une maladie à virus du type polyédrose.

Avant d'envisager les insectes parasites il y a lieu de citer, parmi les ennemis naturels, les oiseaux qui s'attaquent surtout aux chrysalides. Malheureusement ils sont

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de moins en moins nombreux malgré les mesures prises en Sarre pour favoriser leur développement. Nous devons rappeler à ce sujet qu'en Amérique avant 1880 l'espèce voisine *Ennomos subsignaria* causait chaque année d'assez gros dégâts et seule l'acclimatation du *Passer domesticus* (Graham, 1952) permit à partir de cette date de rétablir l'équilibre biologique; cependant on a dû noter des recrudescences des arpeuteuses notamment en 1908-09, les oiseaux ne suffisant pas à rétablir l'équilibre biologique rompu en faveur du dévastateur.

Les hyménoptères parasites ont été nombreux et pour les classer du point de vue biologique nous envisagerons successivement ceux qui s'attaquent aux oeufs, aux chenilles, aux chrysalides.

Comme parasite des oeufs le plus important est le proctotrupide *Aholcus dalmanni* (Ratz.); cet hyménoptère était déjà connu comme parasite des oeufs de l'*Orgyia antiqua*.

Comme parasite des chenilles nous avons récolté un ichneumonide du genre *Eulimneria* et un braconide *Macrocentrus abdominalis* (F.). Ce dernier genre qui présente le phénomène de la polyembryonie a été bien étudié du point de vue biologique: *M. abdominalis* par Voukassovitch qui en 1927 l'a signalé comme parasite des *Psammotis* et des *Tortrix* européens, *M. gifuensis* (Ash.) par Parker (1931); cette espèce parasitant la pyrale du maïs a été introduite en Amérique pour lutter contre cet insecte.

Comme parasite des chrysalides nous avons rencontré deux espèces du genre *Pimpla* et un *Lissonota*. L'une d'elles *Pimpla instigator* (F.) a pu même être filmée en train de pondre dans la forêt dans une chrysalide; cet ichneumonide est connu comme limitant l'extension d'un grand nombre de papillons nuisibles (*Tortrix*, *Orgyia*, *Lymantria*, *Porthetria*, *Thaumetopea*, *Malacosoma*, *Dendrolimus*, etc. et tout récemment on l'a signalé de Hongrie sur *Hyphantria cunea* (Drury).

L'autre appartenant au sous-genre *Apechthis* est le *Pimpla rufata* (Gm.); c'est le plus abondant et il s'attaque en Sarre aussi bien à l'*Ennomos* qu'à *Tortrix viridana* (L.). Il a déjà été cité comme parasitant *T. viridana* (L.) *Lymantria monacha* (L.) et *Malacosoma neustria* (L.).

Le troisième ichneumonide parasite de chrysalides est *Lissonota buolianae* (Hart.), connu parfois sous le nom de *L. transversa* (Bridg.). Suivant Ferrière qui a bien voulu examiner notre matériel les mâles sont des *L. buolianae* typiques tandis que les femelles se rapprochent plus de l'espèce *L. artemisiae* (Tsch.) mais comme il s'agit de la présence ou de l'absence de taches blanches on doit envisager qu'il y a seulement à envisager là des fluctuations d'une même espèce. Comme l'indique son nom cet hyménoptère est connu comme parasite de l'*Evetria buoliana* (Sch.) et comme ce microlépidoptère est bien représenté en Sarre (Stauder, 1955) il n'y a rien d'étonnant à ce que le parasite ait passé d'*Evetria* à *Ennomos*.

Les parasites les plus importants de notre géométride sont sans conteste les diptères tachinidés; suivant Mesnil (1955) qui a bien voulu examiner notre matériel aucun parasite de cette famille n'était connu à ce jour comme parasite de l'*Ennomos quercinaria*.

L'espèce la plus fréquente est *Ctenophorocera pavidia* (Meigen); on doit remarquer que les exemplaires que nous avons élevés au laboratoire sont petits, souvent incomplètement développés et suivant l'éminent entomologiste précité semblent indiquer une adaptation récente à l'*Ennomos quercinaria*. Nous devons rapprocher de cette remarque au sujet du développement le fait que beaucoup de pupes n'ont pas pu éclore comme si l'imago avait avorté. Les hôtes de *Ctenophorocera pavidia* sont très nombreux ce sont surtout des papillons (Mesnil, 1955); on vient de signaler cette espèce en Hongrie (1953) comme parasite de la fameuse écaille fileuse *Hyphantria cunea* (Drury); c'est une espèce à oeufs microtypes déposés sur la cuticule de l'hôte (type I de Pantel); elle est manifestement polyphage.

La deuxième espèce fréquente est *Blondelia nigripes* (Fal); elle est, elle aussi, connue comme polyphage de nombreux papillons (*Lymantria*, *Plusia*, *Porthetria*, *Thaumetopea*, *Dendrolimus*, etc.) et suivant Townsend aurait au moins trois générations par an. Par ses oeufs cette espèce appartient au type VII de Pantel.



Deux autres espèces de tachinides appartiennent au genre *Phryxe* leurs oeufs éclos ou sur le point d'éclore sont déposés sur le corps de la chenille (groupe VI de Pantel).

L'une *Phryxe nemea* (Meigen) connue déjà comme parasite de divers lépidoptères (*Pieris*, *Abraxas*, *Taeniocampa*, etc.), l'autre moins fréquente *Phryxe longicauda* (Wainw.) passe pour une espèce rare; décrite d'Ecosse elle a été retrouvée en Suisse, France et Allemagne. Les hôtes connus sont surtout des lépidoptères (*Operophthera brumata* (L.), *Eupithecia helveticaria* (Boisd.), *Selenia bilunaria* (Esp.), diverses *Zygaena*, *Pieris*, etc.).

Il est vraisemblable que malgré leur multiplication intensive ces divers insectes parasites ne seraient pas parvenus à rétablir à eux seuls l'équilibre biologique si une maladie à virus du type polyédrose n'était pas survenue en 1954 décimant les chenilles arpenteuses au maximum de leur densité d'invasion. Fin juin nous pouvions observer que la plus grande partie des chenilles pendaient le corps flasque ou plus ou moins desséché, accrochées le plus souvent par leurs vraies pattes à leurs fils suspendus soit aux branches soit aux aspérités du fût des arbres. Immédiatement le rapprochement entre ce que nous observions et le syndrome caractéristique de la polyédrose de la Nonne (Wipfelkrankheit, Wilt Disease) s'imposa.

Des frottis nous révélèrent, au laboratoire la présence de myriades de corpuscules brillants subpolyédriques sans affinités pour les colorants usuels. Nous étions donc bien en présence de ce type de maladie épidémique d'une extrême virulence capable de décimer en un temps très court d'immenses populations de chenilles: une virose du type polyédrose était en train d'anéantir sous nos yeux, d'une façon spectaculaire, les chenilles d'*Ennomos* qui approchaient de leur complet développement et qui de ce fait avaient déjà dévoré toutes les frondaisons de cette forêt centenaire; les dommages étaient faits mais on pouvait augurer que l'année suivante, la polyédrose ayant supprimé la grande majorité des *Ennomos*, les arbres n'auraient plus à redouter l'attaque de ces arpeuteuses.

Le virus déterminant la polyédrose que nous avons rencontrée en Sarre chez les chenilles arpeuteuses d'*Ennomos quercinaria* rentre dans le genre *Borrelina* et en raison de sa localisation géographique nous l'avons nommé *Borrelina (Bollea) saraviensis*.

Pour la géométride *Ennomos quercinaria* (Hfn.) le processus avait donc été le même que pour bien d'autres lépidoptères défoliateurs: gradation de l'invasion des arpeuteuses pendant trois années puis polyédrose. Tout permet de penser que la pullulation en 1917 de ces mêmes chenilles dans la même forêt avait dû être stoppée, elle aussi, par une maladie à virus du type polyédrose.

Des nombreuses recherches l'année suivante (1955) permirent de recueillir seulement 6 chenilles d'*Ennomos*; leur élevage au laboratoire nous révéla que trois d'entre elles étaient atteintes de polyédrose et qu'une quatrième était parasitée par la tachinide *Ctenophorocera pavidus* (Meig.); il n'en résulta que deux imagos. En 1956 aucune chenille arpeuteuse de l'espèce *Ennomos quercinaria* n'a été récoltée.

Cet exemple de l'invasion des chenilles dévastatrices de feuillus d'*Ennomos quercinaria* anéantie après trois ans de gradation par une maladie à polyédres vient s'ajouter aux exemples de viroses efficaces déjà connues et souligne l'importance décisive des viroses pour le rétablissement d'un équilibre biologique momentanément rompu par la pullulation d'un ravageur, équilibre que la multiplication intensive naturelle des insectes parasites n'arrivait pas à rétablir.

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Section  
on  
**BIOLOGICAL CONTROL**



Section Editor  
A. B. BAIRD



**INDEX**

	Pages
Reviews of Work in Biological Control . . . . .	443-532
Biological Control of Weeds . . . . .	533-566
Role of Ants in Biological Control . . . . .	567-596
Orchard Mites and Their Natural Control . . . . .	597-674
Utilization of Microorganisms in Insect Control . . . . .	675-710
Insect Pathology . . . . .	711-742
Adaptations of Parasites in Biological Control . . . . .	743-776
Biological Control of the Balsam Woolly Aphid . . . . .	777-826
General Papers . . . . .	827-924

*The following papers were presented at the Congress but are not included herein*

Problems in Latency Phenomenon of Insect Virus

By G. H. BERGOLD

Insect Pathology Laboratory

Sault Ste. Marie, Ont.

Inhibition of the Development of the Fruit-Fly,  
*Drosophila melanogaster*, by Podophyllotoxin

By E. D. GOLDSMITH

New York University

New York, N.Y.

Les Problèmes de la Lutte biologique en Europe et dans le  
Bassin méditerranéen: Activité de la C. I. L. B.

Par PIERRE GRISON

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# The Biological Control of Insect Pests in the Continental United States

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## ABSTRACT

The first insect parasite successfully imported into the United States for the control of an agricultural pest was established on the imported cabbage worm in 1884 as a result of importations from England. Since that time approximately 500 species of parasites and predators from many parts of the world have been imported and released in the field against more than 90 pest species, some in exceedingly large numbers and others in numbers probably too small to give a fair chance of establishment. Of this total, between 95 and 100 species have become established and have contributed in greater or lesser degree to control their hosts.

The most successful projects, from the point of view of effectiveness in control, have been on the browntail moth in New England, the satin moth in New England, and the Pacific Northwest, the oriental moth in Connecticut, the alfalfa weevil in the western states, the Comstock mealybug in the northeastern states, and the cottony cushion scale, black scale, nigra scale, citrophilus mealybug, and grape leaf skeletonizer in California. Field control of the alfalfa caterpillar in the latter state has been accomplished through the application of a polyhedrosis virus in spray or dust form.

This account of accomplishments in the biological control of insect pests in the United States will include reference only to the major problems that have been undertaken and on which some degree of control has been attained. For detailed information regarding all activities along this line, those interested are referred to a recent publication by the United States Department of Agriculture (Clausen, C. P., *Tech. Bull.* 1139, 151 pp. 1956).

Aside from a few rather haphazard proposals of measures to increase the distribution and possible effectiveness of certain native parasites, the first real attempt at biological control was during 1875-84, when *Apanteles glomeratus* (L.) was introduced from England for control of the imported cabbage worm. It became established and quickly spread over a large portion of the country, though contributing little to field control of the pest.

The beginning of sustained work in biological control may be said to date from 1888-89, this period covering Albert Koebele's trip to Australia for the United States Department of Agriculture and his second trip, for that Department and the California State Commission of Horticulture, to Australia, New Zealand, and Fiji in 1891-92. The benefits from these two trips were exceptional, comprising establishment in California of the vedalia beetle, *Rodolia cardinalis* (Muls.), and the dipterous parasite, *Cryptochaetum iceryae* (Will.), on the cottony cushion scale, *Cryptolaemus montrouzieri* Muls., the mealybug predator, and the four scale insect predators, *Lindorus lophantae* (Blaisd.), *Orcus chalybeus* (Boisd.), *Rhizobius debilis* Blackb. and *R. ventralis* (Er.).

The large-scale program of the United States Department of Agriculture on other crop pests began in 1905 with the initiation of a program for the importation of natural enemies of the gypsy and browntail moths. The peak of federal importation activities was attained in the 1920's and early 1930's when the large-scale programs on the European corn borer, Japanese beetle, oriental fruit moth, sugarcane borer and several forest pests were underway.

The University of California has had an importation program under way for many years, with the main emphasis placed on natural enemies of scale insects and mealybugs attacking citrus and deciduous fruit trees, but extended in recent years to include a series of field crop insects.

A total of 485 species of imported parasites and predators have been colonized in the United States against at least 77 pest species. Of these, at least 95 species have



been established since the initial success with *A. glomeratus* in 1884. Nearly half (42) of these species originated in various parts of Europe, 13 in Australia, 10 in South Africa and 9 in Japan. Eighty-one of these species are parasitic in habit and 14 predaceous. Thirty-one species are of the families Encyrtidae and Eulophidae, reflecting mainly the long-term work on scale insects and mealybugs in California, and 15 are Tachinidae, 15 Braconidae, 7 Ichneumonidae, and 11 Coccinellidae.

It might be informative to summarize briefly the present status of the pest insects against which biological control measures have proven partially or fully successful in the continental United States. These are as follows:

#### LEPIDOPTERA

BROWN-TAIL MOTH: *Nygmia phaeorrhoea* (Donov.). Seven parasites of this pest have been established in New England, of which the most important are *A. lacteicolor* Vier. and *Townsendiellomyia nidicola* (Tns.). The progress and effectiveness of these parasites was not closely followed in the early years so that their value in control was not accurately determined by field studies. However, the pest has declined to a position of very minor importance since their introduction and there is every reason to credit them with a substantial role in control.

GYPSY MOTH: *Porthetria dispar* (L.). It has been exceedingly difficult to evaluate the results of the parasite introduction program against this pest. Two egg parasites, 6 that attack the larva and 1 the pupa, as well as 2 predators, are well established. The most effective among the larval parasites are *Compsilura concinnata* (Meig.), *Blephoripoda scutellata* (R.-D.) and *A. melanoscelus* (Ratz.). Aggregate mortality of the immature stages is often high, yet the peak infestations in recent years have been nearly as high as during the period preceding parasite introduction. The frequency of these outbreaks have been reduced and the extent of tree defoliation lessened over the infested area as a whole.

SATIN MOTH: *Stilpnotia salicis* (L.). The larval parasites, *A. solitarius* (Ratz.) and *Meteorus versicolor* (Wesm.), obtained from Europe have proven to be highly effective against this pest in New England and the Pacific Northwest. Satisfactory control was attained by *M. versicolor* in Washington and a very substantial reduction in the infestations in New England was brought about by *A. solitarius*, aided by *C. concinnata*.

ORIENTAL MOTH: *Cnidocampa flavescens* (Wlkr.). This pest is a defoliator of certain shade and ornamental trees in a small area centering about Boston. The introduction of the tachinid parasite *Chaetexorista javana* B. & B. from Japan in 1929-30 was quickly followed by the decline of the pest to a non-injurious status. It developed later that the occasional very cold winters were exceedingly injurious to the parasite and that the pest insect developed to an injurious status following such winters. The parasite recovers quickly however, and the usual excellent control is soon re-established.

EUROPEAN CORN BORER: *Pyrausta nubilalis* (Hbn.). The program for importation of parasites of this pest extended from 1919 to 1938 and was on a very large scale. Six species have become established, of which *Lydella stabulans grisescens* R.-D. and *Macrocentrus gifuensis* Ashm. are the most important. All species are sharply limited by their ecological requirements, so that none is established throughout the infested area. *Macrocentrus* has persisted in substantial numbers only in certain areas of southern New England, and *Lydella* in parts of the Eastern and Middle Atlantic States and in the Mississippi and Ohio River Valleys, where field parasitization may range from 45 to 75 per cent. Full control has not been attained in any area.

ORIENTAL FRUIT MOTH: *Grapholitha molesta* (Busck). The extensive program for the importation of parasites of this pest from Japan and Korea during 1930-39 resulted in the establishment of only a single species, *Agathis diversus* (Mues.), and it has been recovered at only a few points and contributes nothing to control of the pest. However, a native parasite *Macrocentrus ancylivorus* Roh., the normal host of

which is the strawberry leaf roller, and which occurred commonly only in the New Jersey area, quickly adapted itself to the new host. From 1929 onwards it was reared in large numbers and distributed to all infested states, and brought about a marked reduction in fruit infestation in practically all areas. Periodic release of 10 females per tree proved to be highly successful during occasional seasons and in some areas where winter carry-over was not in sufficient numbers to give reasonable protection to the peach crop.

**ALFALFA CATERPILLAR:** *Colias philodice eurytheme* Bdv. Attempts at biological control of this pest have centered around use of the endemic virus, *Borrelina compeoles* Steinhaus. Water suspensions or dusts containing the virus, and applied by any conventional method, have yielded excellent control in 7 to 9 days. Also, suspensions or dusts of *Bacillus thuringiensis* Berliner have proven to be even more effective, giving a very high mortality within 2 to 3 days after application.

**WESTERN GRAPE LEAF SKELETONIZER:** *Harrisina brillians* B. & McD. Full field control of this pest in San Diego County, California, was obtained through the importation from Arizona and establishment of two larval parasites, *Apanteles harrisinae* Mues. and *Sturmia* sp., aided by an unidentified granulosus virus that effects a high mortality of the early larval stages.

### COLEOPTERA

**JAPANESE BEETLE:** *Popillia japonica* Newm. Four parasites of the grubs and one that attacks the adult beetles were established in the eastern United States as a result of importations from Japan and Korea during the 1920's. Only one of these, *Tiphia vernalis* Roh., has proven to be of appreciable value in the field. It is now widely distributed and often effects a parasitization of the grubs of 50 per cent or more.

Probably the most effective of the biological control agents operating against this pest is the milky disease, caused by *Bacillus popilliae* Dutky. Dust preparations of the spores of this organism are available commercially, and when properly applied can be depended upon to reduce the grub populations in the soil to a non-injurious level and to hold them at that level thereafter.

**ALFALFA WEEVIL:** *Hypera postica* (Gyll.). The importation from Italy in 1911-13 and the establishment in Utah of *Bathyplectes curculionis* (Thoms.) resulted in field parasitization often exceeding 90 per cent, and this, in conjunction with a change in cutting practices, has very greatly reduced the damage to the crop. The later establishment of the parasite in lowland middle California resulted in reduction of the pest infestations to a very low level, whereas it was not nearly so effective in the San Joaquin Valley.

### HEMIPTERA

**WOOLLY APPLE APHID:** *Eriosoma lanigerum* (Hausm.). The introduction of *Aphelinus mali* Hald. from New England into the Pacific Northwest resulted in full control of the pest, an outcome identical with that attained in many other countries. An added and substantial benefit in this area was the elimination of perennial apple canker as a serious problem. The colonies of aphids at pruning scars and other wounds provided conditions favorable for development of canker lesions, and control of the aphid by *Aphelinus* has eliminated the conditions essential for development of the disease.

**COTTONY CUSHION SCALE:** *Icerya purchasi* Mask. The importation of the vedalia beetle, *R. cardinalis*, from Australia in 1888-89, and its rapid distribution through the infested citrus groves of southern California, resulted in complete control within 15 months after the arrival of the first shipment. This condition has persisted to the present time, except in orchards where the new insecticides, notably DDT, have been applied for control of other pests.

A dipterous internal parasite, *Cryptochaetum iceryae* (Will.), was introduced and established at the same time. It appears capable, alone, of controlling the pest in the coastal areas, but its activities have largely gone unnoticed, it being completely overshadowed by the more conspicuous vedalia beetle.

CITRUS MEALYBUG: *Pseudococcus citri* (Risso.). The first introduction against this pest was the Australian beetle, *C. montrouzieri* Muls., in 1891-92. It proved effective in reducing heavy infestations but failed to carry over the winters in appreciable numbers. Accordingly, for a period of years, it was reared by the millions in insectaries and released in the orchards each season whenever the mealybug infestations became sufficiently heavy to warrant it. Later, in 1914, *Leptomastidea abnormis* (Gir.) was imported from Sicily. These two natural enemies have reduced the severity of the infestations, though occasional outbreaks still occur in the coastal counties.

CITROPHILUS MEALYBUG: *Pseudococcus gahani* Green. This has been one of the most successful of the biological control efforts in California, equalling that on the cottony cushion scale. The introduction of *Coccophagus gurneyi* Comp. and *Tetracnemus pretiosus* Timb. from Australia in 1928 and their distribution throughout the citrus orchards of southern California resulted in early and complete suppression of the pest to the point where it became difficult to find even single specimens. Contrary to the course of events with other pests normally under biological control, the application of DDT and other new and highly toxic insecticides has not resulted in a single instance of build up of the citrophilus mealybug in the orchards.

LONG-TAILED MEALYBUG: *Pseudococcus adonidum* (L.). Three parasites of this pest all imported in the 1930's, are now established in southern California; *Anarhopus sydneyensis* Timb. from Australia, *Tetracnemus peregrinus* Comp. from Brazil, and *Anagyrus fusciventris* (Gir.) from Hawaii. These have aided in control of the pest in citrus groves in the coastal areas of the state, though localized slight outbreaks occur from time to time.

COMSTOCK MEALYBUG: *Pseudococcus comstocki* (Kuw.). This species, native of Japan, became a serious pest of apple in the eastern United States during the 1930's. Its parasites were imported from that country in 1939-41, the most important of them being *Allotropa burrelli* Mues. and *Pseudaphycus malinus* Gahan. In addition, another effective species, *Clausenia purpurea* Ishii, from that country was already present in some of the infestations, it apparently having been brought into the United States with the original mealybug stock. These three species have been fully effective in reducing the infestations throughout the northeastern states to a non-injurious level.

BLACK SCALE: *Saissetia oleae* (Bern.). Efforts directed towards biological control of the black scale in California have been underway since 1890 and during the intervening period 8 species of internal parasites, 2 chalcidoid egg predators and 2 coccinellid predators, mostly from South Africa and Australia, have been imported and established. Results were relatively slight until the importation of *Aphycus helvolus* Comp. from South Africa in 1938. This species proved to be highly effective and brought the pest under control in most sections of southern California. It developed later, however, that the parasite is unable to withstand the occasional colder than normal winters of that area, and that outbreaks of the scale consequently develop during the seasons following such winters. In spite of this periodic ineffectiveness however, *Aphycus* has saved the citrus growers of California millions of dollars.

NIGRA SCALE: *Saissetia nigra* (Nietn.). The biological control of the nigra scale in southern California was a byproduct of the work on the black scale. The colonies of *A. helvolus* released in citrus orchards during 1938 and following years for control of the latter pest quickly spread to the heavy infestations of nigra scale on shade and ornamental trees in the vicinity. Full commercial control was quickly attained and the infestations have remained at a very low level since that time. The parasite has been much more consistent in its control of this pest than of the black scale.

CALIFORNIA RED SCALE: *Aonidiella aurantii* (Mask.). Efforts directed towards the biological control of this destructive pest of citrus in California have been under way continuously since 1890, and the tropical and subtropical regions of the world have been combed for parasites and predators that might aid in its control. Seven species of these have been established in the state but it was only in 1947, when *Aphytis lingnanensis* Comp. was obtained from South China, that definite progress

could be reported. This species has aided substantially in controlling the pest under the mild climatic conditions of the coastal counties. It is ineffective in the interior valleys where summer temperatures often exceed 100°F., and with very low relative humidity, and in winter may hold below 45°F. for several days at a time. Under both of these conditions there is a high mortality of all stages of the parasite.

**YELLOW SCALE:** *Aonidiella citrina* (Coq.). In general, the parasites and predators that attack the California red scale likewise develop on the yellow scale, but with important exceptions. The physiological race of *Comperiella bifasciata* How. that is restricted to the yellow scale was obtained from Japan in 1924-25 and has effectively controlled the pest in southern California, but has not been so successful against the pest in the citrus-producing areas of the San Joaquin Valley.

**PURPLE SCALE:** *Lepidosaphes beckii* (Newm.). The purple scale has long been one of the most destructive pests of citrus in the coastal counties of southern California. The importation of natural enemies was begun in the 1890's and many species have been reared and tested during the intervening time, but with very little success. It was only very recently, when *Aphytis lepidosaphes* Comp. was obtained from South China and Formosa in 1948-49 and *Phycus* "B" from Formosa in 1950-51, that the outlook became at all encouraging. These species, especially *A. lepidosaphes*, have shown a capacity to control the pest and a number of orchards having heavy infestations have shown satisfactory clean-up of the scale.

**OLIVE SCALE:** *Parlatoria oleae* (Colvée). This scale is a very serious pest of olive, various deciduous fruit trees and a wide range of ornamentals in California. The importation of *Aphytis maculicornis* (Masi) from Iran in 1951 and its establishment in the olive orchards of the state was highly beneficial and in many orchards reduced the pest population 90-95 per cent. This provided adequate protection from injury to the trees, but unfortunately the few remaining scale of the second generation settle mainly upon the fruit, so that a considerable portion of the crop must still be discarded as culls or utilized in production of olive oil, which is much less profitable than marketing of the fruit.





# Successful Biological Control Against Animals<sup>1</sup>

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Biological control is a recognized method of combating crop pests and is rapidly increasing in importance. An analysis of the success that has been achieved may help us to understand and appreciate the problems involved.

This analysis will be confined to biological control attempts through the use of parasites and predators against various animal pests. A similar analysis was made 20 years ago (Sweetman 1935, 1936). Twenty-six pest species were listed as under commercial control at that time. Time has shown that one example was in error, as the control was temporary only. More recent information has brought to light 12 other successful cases that existed during the period covered.

Much progress in biological control has been made during the intervening period. Only those instances which are highly successful or decidedly beneficial to the extent of eliminating or greatly reducing other methods of control are included. Probably most workers will agree with the examples offered, but some would wish to add many more instances as successful. Instances which are temporary or slightly successful only, as the reduction or near eradication of white grubs from a field by birds during cultivation, are not included, since results may be vastly different in nearby fields or the following season. The exclusion of such temporary or local examples of control should not overshadow their importance, however, as it is possible that such instances in the aggregate are of greater importance than that of the examples given.

A list of successful cases of control with the supporting evidence follows:

Pest Species Order and Family	Beneficial Species Order and Family	Parasite or Predator	Countries or Regions
1. <i>Popillia japonica</i> Newm. Col, Sca	<i>Bacillus popilliae</i> (Dutky) Eub, Ba	Parasite	Eastern United States
2. <i>Colias philodice</i> <i>eurytheme</i> (Bdvl.) Lep, Pi	<i>Borrelina campeoles</i> (Stein.) V, Bo	Parasite	California
3. <i>Diprion hercyniae</i> (Htg.) Hy, Dip	Virus V <i>Drino bohémica</i> (Mesn.) D, Ta <i>Exenterus vellicatus</i> (Cush.) D, Ta	Parasite  Parasite	Eastern Canada, Maine
4. <i>Neodiprion</i> <i>sertifer</i> (Geoff.) Hym, Dip	Virus V	Parasite	Eastern Canada, Eastern United States
5. <i>Oryctolagus cuniculus</i> La, Lep	Myxoma virus V	Parasite	Australia
6. <i>Pseudococcus nipae</i> (Mask.) Ho, Co	<i>Pseudaphycus utilis</i> (Timb.) Hy, En	Parasite	Hawaiian Islands
7. <i>Pseudococcus</i> <i>filamentosus</i> (Ckll.) Ho, Co	<i>Anagyrus dactylopii</i> (How.) Hy, En	Parasite	Hawaiian Islands

<sup>1</sup>The data in this paper will be included in: The Principles of Biological Control to be published in 1958 by Wm. C. Brown of Dubuque, Iowa.

8.	<i>Pseudococcus maritimus</i> (Ehrh.) Ho, Co	<i>Acerophagus notativentris</i> (Gir.) Hy, En	Parasite	California
9.	<i>Pseudococcus comstocki</i> (Kuw.) Ho, Co	<i>Pseudaphycus malinus</i> (Gahan) Hy, En <i>Allotropa burrelli</i> (Mues.) Hy, Pl	Parasite Parasite	Ohio
10.	<i>Trionymus boninsis</i> (Kuw.) Ho, Co	<i>Aphycus terryi</i> (Full.) Hy, En	Parasite	Hawaiian Islands
11.	<i>Trionymus sacchari</i> (Ckll.) Ho, Co	<i>Anagyrus saccharicola</i> (Timb.) Hy, En	Parasite	Hawaiian Islands
12.	<i>Pseudaulacaspis pentagona</i> (Targ.) Ho, Co	<i>Prospaltella berlesei</i> (How.) Hy, Eu	Parasite	Italy
13.	<i>Eulecanium coryli</i> (L.) Ho, Co	<i>Blastothrix sericea</i> (Dalm.) Hy, En	Parasite	British Columbia
14.	<i>Asterolecanium variolosum</i> (L.) Ho, Co	<i>Habrolepis dalmani</i> (Westw.) Hy, En	Parasite	New Zealand
15.	<i>Furcaspis oceanica</i> (Ldgr.) Ho, Co	<i>Anabrolepis oceanica</i> (Doutt) Hy, En	Parasite	Caroline Islands
16.	<i>Aonidiella citrina</i> (Coq.) Ho, Co	<i>Comperiella bifasciata</i> (How.) Hy, En	Parasite	California, Texas
17.	<i>Chrysomphalus aonidum</i> (L.) Ho, Co	<i>Pseudhomalopoda prima</i> (Gir.) Hy, En <i>Prospaltella aurantii</i> (How.) Hy, Eu <i>Aspidiotiphagus lounsburyi</i> (B. & P.) Hy, Eu <i>Aspidiotiphagus citrinus citrinus</i> (Craw.) Hy, Eu	Parasite Parasite Parasite Parasite	Florida
18.	<i>Coccus hesperidum</i> (L.) Ho, Co	<i>Aphycus luteolus</i> (Timb.) Hy, En	Parasite	California
19.	<i>Ceroplastes rubens</i> (Mask.) Ho, Co	<i>Anicetus beneficus</i> (Ishii) Hy, En	Parasite	Japan
20.	<i>Parlatoria oleae</i> (Colvee) Ho, Co	<i>Aphytis</i> sp. Hy, Eu	Parasite	California
21.	<i>Trialeurodes vaporariorum</i> (Westw.) Ho, Al	<i>Encarsia formosa</i> (Gah.) Hy, Eu	Parasite	Canada, California

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|-----|---|--|----------|---|
| 22. | <i>Aleurocanthus spiniferus</i><br>(Quaint.) Ho, Al | <i>Prospaltella smithi</i><br>(Silv.) Hy, Eu         | Parasite | Japan   |
|     |   | <i>Prospaltella smithi</i><br>(Silv.) Hy, Eu         | Parasite | Guam  |
|     |   | <i>Amitus hesperidum</i><br>(Silv.) Hy, Pl           | Parasite |   |
| 23. | <i>Saissetia nigra</i><br>(Nietn.) Ho, Co           | <i>Aphycus helvolus</i><br>(Comp.) Hy, En            | Parasite | Southern California   |
| 24. | <i>Saissetia oleae</i><br>(Bern.) Ho, Co            | <i>Aphycus lounsburyi</i><br>(How.) Hy, En           | Parasite | California before 1940  |
|     |   | <i>Aphycus helvolus</i><br>(Comp.) Hy, En            | Parasite | California since 1940   |
|     |   | <i>Lecaniobius utilis</i><br>(Comp.) Hy, Eup         | Parasite | Peru  |
|     |   | <i>Aphycus lounsburyi</i><br>(How.) Hy, En           | Parasite |   |
|     |   | <i>Scutellista cyanea</i><br>(Mots.) Hy, Pt          | Predator |   |
|     |   |  |          |   |
| 25. | <i>Eriosoma lanigerum</i><br>(Hausm.) Ho, Ap        | <i>Aphelinus mali</i><br>(Hald.) Hy, Eu              | Parasite | New Zealand,<br>South Africa,<br>Northwest<br>United States,<br>Japan, etc. |
| 26. | <i>Pseudococcus gahani</i><br>Green Ho, Co          | <i>Cryptolaemus montrouzieri</i><br>(Muls.) Col, Coc | Predator | California largely before 1930  |
|     |   | <i>Coccophagus gurneyi</i><br>(Comp.) Hy, Eu         | Parasite | California since 1930   |
|     |   | <i>Tetracnemus pretiosus</i> (Timb.)<br>Hy, En       | Parasite |   |
| 27. | <i>Pseudococcus citri</i><br>(Risso) Ho, Co         | <i>Leptomastidea abnormis</i> (Gir.) Hy, En          | Parasite | California  |
|     |   | <i>Cryptolaemus montrouzieri</i><br>(Muls.) Col, Coc | Predator |   |
| 28. | <i>Pinnaspis minor</i><br>Ho, Co                    | <i>Aspidiotiphagus citrinus</i> (Craw.)<br>Hy, Eu    | Parasite | Peru  |
|     |   | <i>Arrhenophagus chionaspidis</i> (Auri.)<br>Hy, En  | Parasite |   |
|     |   | <i>Microweisia</i><br>(Scymnus) sp.<br>Col, Coc      | Predator |   |
|     |   |  |          |   |



34. <i>Aleurocanthus woglumi</i> (Ashby) Ho, Al	<i>Eretmocerus serius</i> (Silv.) Hy, Eu	Parasite	Jamaica, Haiti, Panama, Costa Rica, West Coast of Mexico
	<i>Eretmocerus serius</i> (Silv.) Hy, Eu	Parasite	Cuba, Bahama Islands
	<i>Catana clauseni</i> (Chapin) Col, Coc	Predator	
35. <i>Aspidiotus destructor</i> (Sign.) Ho, Co	<i>Cryptognatha nodiceps</i> (Mshl.) Col, Coc	Predator	Fiji Islands
	<i>Chilocorus politus</i> (Muls.) Col, Coc	Predator	Mauritius
	<i>Chilocorus nigritus</i> (Muls.) Col, Coc	Predator	
	<i>Chilocorus politus</i> (Muls.) Col, Coc	Predator	Java, Bali, etc.
	<i>Aspidiotiphagus citrinus</i> (Cwfd.) Hy, Eu	Parasite	
36. <i>Eriococcus coriaceus</i> (Mask.) Ho, Co	<i>Rhizobius ventralis</i> (Erich.) Col, Coc	Predator	New Zealand
37. <i>Pinnaspis buxi</i> Bouche Ho, Co	<i>Telsimia nitida</i> (Chapin) Col, Coc	Predator	Hawaiian Islands
38. <i>Asterolecanium bambusae</i> (Bdvl.) Ho, Co <i>Asterolecanium militaris</i> (Bdvl.) Ho, Co <i>Asterolecanium pustulans</i> (Ckll.) Ho, Co <i>Pseudaulacaspis pentagona</i> (Targ.) Ho, Co	<i>Chilocorus cacti</i> (L.) Col, Coc	Predator	Puerto Rico, Haiti
	<i>Cladis nitidula</i> (F.) Col, Coc	Predator	
39. <i>Ischnaspis longirostris</i> (Sign.) Ho, Co <i>Chrysomphalus ficus</i> (Ash.) Ho, Co <i>Eucalymnatus tessellatus</i> (Sign.) Ho, Co <i>Pinnaspis buxi</i> (Bouche) Ho, Co	<i>Chilocorus distigma</i> (Klug.) Col, Coc	Predator	Seychelles Islands
	<i>Exochomus ventralis</i> (Gerst.) Col, Coc	Predator	
	<i>Exochomus flavipes</i> (Thun.) Col, Coc	Predator	
	<i>Chilocorus nigritus</i> (Muls.) Col, Coc	Predator	
40. Scale insects Ho, Co	<i>Cryptolaemus montrouzieri</i> (Muls.) Col, Coc	Predator	Celebes
41. <i>Aphis sacchari</i> (Zehnt.) Ho, Ap	<i>Coelophora inaequalis</i> (Fabr.) Col, Coc	Predator	Hawaiian Islands since 1930



42.	<i>Tarophagus proserpina</i> (Kirk.) Ho, Cic	<i>Cyrtorhinus fulvus</i> (Knight) He, Mi	Predator	Hawaiian Islands, Guam
43.	<i>Perkinsiella</i> <i>saccharicida</i> (Kirk.) Ho, Cic	<i>Cyrtorhinus mundulus</i> (Bredd.) He, Mi	Predator	Hawaiian Islands since 1923
44.	<i>Brentispa mariana</i> (Spaeth) Col, Hi	<i>Tetrastichus</i> <i>brontispae</i> (Ferr.) Hy, Eu	Parasite	Mariana Islands
45.	<i>Phyllotreta</i> <i>striolata</i> (F.) <i>P. bipustulata</i> (F.) Col, Chr	<i>Microtonus vittatae</i> (Mues.) Hy, Br	Parasite	Northern United States, Canada
46.	<i>Cassida vittata</i> (de Vill.) Col, Chr	<i>Tetrastichus</i> <i>bruzzonis</i> (Cwfd.) Hy, Eu	Parasite	Italy
47.	<i>Promecotheca reichei</i> (Baly) Col, Chr	<i>Pleurotropis parvulus</i> (Ferr.) Hy, Eu	Parasite	Fiji Islands
48.	<i>Promecotheca</i> <i>nuciferae</i> (Maulik) Col, Chr	<i>Pleurotropis</i> <i>parvulus</i> (Ferr.) Hy, Eu <i>Dimmockia javanica</i> (Ferr.) Hy, Eu	Parasite Parasite	Java
49.	<i>Anomala orientalis</i> (Waterh.) Col, Sca	<i>Campsomeris</i> <i>marginella modesta</i> Sm. Hy, Sco <i>Tiphia segregata</i> (Cwfd.) Hy, Ti	Parasite Parasite	Hawaiian Islands
50.	<i>Oryctes tarandus</i> (Oliv.) Col, Sca	<i>Scolia oryctophaga</i> (Coq.) Hy, Sco	Parasite	Mauritius
51.	<i>Syagrius fulvitaris</i> (Pasc.) Col, R	<i>Doryctes syagrii</i> (Full.) Hy, Br	Parasite	Hawaiian Islands
52.	<i>Gonipterus</i> <i>scutellatus</i> (Gyll.) Col, R	<i>Patasson nitens</i> (Gir.) Hy, My	Parasite	New Zealand, Africa, Madagascar, Mauritius
53.	<i>Rhabdoscelus obscura</i> (Boisd.) Col, R	<i>Microceromasia</i> <i>sphenophori</i> (Vill.) D, Ta	Parasite	Hawaiian Islands
54.	<i>Argyrotaenia citrana</i> (Fern.) Le, To	<i>Meteorus argyrotaeniae</i> (Joh.) Hy, Br	Parasite	Washington
55.	<i>Chilo suppressalis</i> (Wlk.) Le, Cra	<i>Trichogramma japonicum</i> (Ash.) Hy, Tr <i>Amyosoma chilonis</i> (Vier.) Hy, Br <i>Diocetes chilonis</i> (Cush.) Hy, I	Parasite Parasite Parasite	Hawaiian Islands

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|-----|--|---|--|---|
| 56. | <i>Levuana iridescens</i><br>(Beth.-Baker) Le, Z   | <i>Ptychomyia remota</i><br>(Ald.) D, Ta  | Parasite   | Fiji Islands  |
| 57. | <i>Pyrausta nubilalis</i><br>(Hbn.) Le, Py   | <i>Lydella stabulans</i><br><i>grisescens</i> R. D.<br>D, Ta  | Parasite   | Guam, 1932 to<br>about 1940   |
| 58. | <i>Pseudaletia unipuncta</i><br>(Haw.) Le, Pha   | <i>Euplectrus</i><br><i>plathypenae</i> (How.)<br>Hy, Eu<br><i>Archytas cirphis</i><br>(Cur). D, Ta   | Parasite<br><br>Parasite                                 | Hawaiian Islands  |
| 59. | <i>Laphygma exempta</i><br>(Wlk.) Le, Pha  | <i>Apanteles marginiventris</i><br>(Cres.) Hy, Br<br><i>Meteorus laphygmae</i><br>(Vier.) Hy, Br<br><i>Telenomus nawai</i><br>(Ash.) Hy, Sce<br><i>Eucelatoria</i><br><i>armigera</i> (Coq.)<br>D, Ta | Parasite<br><br>Parasite<br><br>Parasite<br><br>Parasite | Hawaiian Islands  |
| 60. | <i>Diatraea</i><br><i>saccharalis</i> (F.)<br>Le, Cra  | <i>Paratheresia</i><br><i>claripalpis</i> D, Ta   | Parasite   | Peru  |
| 61. | <i>Diatraea</i><br><i>crambidoides</i><br>(Grote) Le, Cra  | <i>Solenopsis zyloni</i><br>(McC.) Hy, Fo   | Predator   | Southern<br>United States   |
| 62. | <i>Heliothis virescens</i><br>(F.) Le, Pha<br><i>Argyrotaenia</i><br><i>sphaleropa</i><br>Le, To | <i>Paratriphleps laeviusculus</i><br>He, Mi<br><i>Rhinacloa carmelitana</i><br>He, Ant  | Predator<br><br>Predator                                 | Peru  |
| 63. | <i>Pristiphora</i><br><i>erichsonii</i> (Htg.)<br>Hy, Ten  | <i>Mesoleius tenthredinis</i><br>(Morl.) Hy, I  | Parasite   | Maritime<br>Provinces,<br>Quebec,<br>British Columbia,<br>Manitoba<br>before 1940 |
| 64. | <i>Siphanta acuta</i><br>(Wlk.) He   | <i>Aphanomerus pusillus</i><br>(Perk.) Hy, Sce  | Parasite   | Hawaiian Islands  |
| 65. | <i>Axiagastus</i><br><i>campbelli</i> He, Pe   | <i>Oecophylla smaragdina</i><br>(F.) Hy, Fo   | Predator   | Solomon Islands,<br>South China   |
| 66. | <i>Pseudothoraptus</i><br><i>wayi</i> (Brown) He, Cor  | <i>Oecophylla longinoda</i><br>(Latr.) Hy, Fo   | Predator   | East Africa,<br>Zanzibar Island   |
| 67. | <i>Perrisia pyri</i><br>(Bouche) D, C  | <i>Misocyclops marchali</i><br>(Kieff.) Hy, Pl  | Parasite   | New Zealand   |

68.	<i>Dacus dorsalis</i> (Hend.) D, Tep	<i>Opius oophilus</i> (Full.)	Parasite	Hawaiian Islands
		Hy, Br		
		<i>Opius longicaudatus</i> (Ash.) Hy, Br	Parasite	
		<i>Opius incisi</i> (Silv.) Hy, Br	Parasite	
69.	<i>Gryllotalpa africana</i> (Beau.) O, G	<i>Larra luzonensis</i> (Roh.) Hy, Sp.	Parasite	Hawaiian Islands
70.	<i>Oxya chinensis</i> (Thun.) O, Acr	<i>Scelio pambertoni</i> (Timb.) Hy, Sce	Parasite	Hawaiian Islands
71.	<i>Sminthurus viridis</i> (L.) Coll, Sm	<i>Biscirus lapidarius</i> (Kram.) Ac, Bd	Predator	Australia
72.	<i>Latrodectus mactans</i> (Fabr.) Ar, Th	<i>Baeus latrodecti</i> (Doz.) Hy, Sce	Parasite	Hawaiian Islands
73.	<i>Metatetranychus citri</i> (McG.) Ac, Tet	<i>Lindorus lophantae</i> (Blaisd.) Col, Coc	Predator	California
		<i>Chilocorus</i> sp. Col, Coc	Predator	
		<i>Typhlodromus</i> sp. Ac, Ph.	Predator	California
74.	<i>Tarsonemus pallidus</i> (Banks) Ac, Tar	<i>Typhlodromus reticulatus</i> (Oud.) Ac, Ph	Predator	California
		<i>Typhlodromus cucumeris</i> (Oud.) Ac, Ph	Predator	
75.	<i>Achatina fulica</i> (Bow.) Pul, Ach	<i>Gonaxis kibweziensis</i> (Smith) Pul, Str	Predator	Mariana Islands, Islands of Pacific Trust Territory, Hawaiian Islands
76.	Mosquitoes D, Cu	Cyprinodontidae Poeciliidae	Predators	Tropical and semitropical regions
77.	<i>Cnemarachis vandinei</i> (Smyth) Col, Sca	<i>Ameiva exsul</i> Sq, Te	Predator	Puerto Rico, before 1900
	<i>Phyllophaga portoricensis</i> (Smyth) Col, Sca			
78.	<i>Strategus barbigarus</i> (Chap.) Col, Sca	<i>Bufo marinus</i> (L.) An, Bu	Predator	Puerto Rico 1920 to 1940
	<i>Cnemarachis vandinei</i> (Smyth) Col, Sca			
	<i>Phyllophaga portoricensis</i> (Smyth) Col, Sca			

79. <i>Nomadacris</i> <i>septemfasciata</i> (Serv.) O, Acr.	<i>Acridotheres tristis</i> L.) Pa, St	Predator	Mauritius since 1770
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## ABBREVIATIONS

Acarina	Encyrtidae	Pteromalidae
Achatinidae	Eubacteriales	Pulmonata
Acridae	Eulophidae	Pyraustidae
Aleyrodidae	Eupelmidae	Rhynchophora
Anura	Formicidae	Scarabaeidae
Anthocoridae	Fungi Imperfecti	Scelionidae
Aphidae	Fungi	Scolidae
Araneida	Gryllotalpidae	Smynthuridae
Bacillaceae	Hemiptera	Sphexidae
Bdellidae	Hispidae	Squamata
Borelinaceae	Homoptera	Sturnidae
Braconidae	Hymenoptera	Streptaxidae
Bufo	Ichneumonidae	Symphobiidae
Cecidomyiidae	Lagomorpha	Tachinidae
Chrysopidae	Lepidoptera	Tarsonemidae
Chrysomelidae	Leporidae	Teiidae
Cicadellidae	Miridae	Tenthredinidae
Coccidae	Myrmecidae	Tephritidae
Coccinellidae	Neuroptera	Tetranychidae
Coleoptera	Orthoptera	Theridiidae
Collembola	Passeres	Tiphiidae
Cryptochaetidae	Pentatomidae	Tortricidae
Crambidae	Phytoseiidae	Trichogrammatidae
Culicidae	Phalaenidae	Virales
Diptera	Pieridae	Zygaenidae
Diprionidae	Platyasteridae	

Nearly a hundred pests can be listed as being commercially controlled by parasites and predators. A wide variety of pests are involved. Nearly all are arthropods, mostly insects, as shown in the following list:

Homoptera	45	Orthoptera	3	Collembola	1
Coleoptera	15	Hemiptera	3	Araneida	1
Lepidoptera	10	Hymenoptera	3	Mollusca	1
Diptera	7	+ Acarina	2	Mammals	1

The Homoptera are nearly all Coccidae, but include Aleyrodidae, Aphidae and Cicadellidae. These pests are largely sessile during most of the life cycle, or are sedentary or gregarious. Each attacks a limited number of host plants. These characteristics render them especially susceptible to attack by parasites and predators. The Coleoptera are mostly Scarabaeidae and Chrysomelidae, but include Rhynchophora and a hispid. The chrysomelids are exposed to enemies, but the scarabaeids and weevils, particularly the larvae, are more hidden and protected in the environment. The Lepidoptera are mostly attacked as caterpillars, although some are not in the open. Most of the Diptera are mosquitoes, which are attacked as larvae by fish. The balance of the list are largely exposed pests attacked by various invertebrate and vertebrate predators.

The beneficial parasites and predators that have been successful against pests are mostly insects, but mites and snails, and several vertebrates and microorganisms are included. The systematic distribution of the beneficial organisms follows:

Hymenoptera	77	Hemiptera	4
Eulophidae	25	Miridae	3
Encyrtidae	23	Anthocoridae	1
Mymaridae	1	Neuroptera	2
Trichogrammatidae	1	Chrysopidae	1
Eupelmidae	1	Sympherobiidae	1
Pteromalidae	1	Acarina	4
Braconidae	9	Phytoseiidae	3
Ichneumonidae	2	Bdellidae	1
Scelionidae	4	Virus	4
Platygasteridae	3	Insect	3
Scoliidae	2	Vertebrate	1
Tiphidae	1	Vertebrates	5 +
Formicidae	3	Reptilia	1
Sphecidae	1	Amphibia	1
Coleoptera	28	Aves	1
Coccinellidae	28	Pisces	2 +
Diptera	7	Mollusca	1
Tachinidae	6	Bacteria	1
Cryptochaetidae	1	Fungi	1

There is considerable overlapping in the listing as 2 pests of similar habits in an area may be controlled by a single beneficial organism or 2 or more beneficial organisms may be listed as controlling a pest in a particular environment. Five orders of insects containing useful species are shown. The vast majority of beneficial organisms are insects, two-thirds of which are Hymenoptera. Fifty-two of the 77 listings of Hymenoptera belong to the Chalcidoidea, the balance being distributed in 5 superfamilies. About one-fourth of the insect species involve Coleoptera, all being coccinellidae. A few Diptera, Hemiptera and Neuroptera complete the insect listing. Other arthropods include 4 species of mites. One snail appears to deserve mention as a successful predator. The vertebrates include several fish, a lizard, toad and bird. A number of species of fish are quite useful, but the degree of success in natural environments usually requires constant assistance by man and is frequently supplemented with insecticides. Fish are frequently very successful in small artificial pools, tanks, cisterns, and other containers. Other vertebrates, particularly birds, may be successful in certain environments, but data warranting additional examples have not been located. Temporary reduction of local infestations by birds frequently occurs. Microorganisms: viruses, fungi and bacteria are conspicuous for the few selections. Viruses and bacteria are the most important.

About 125 species of organisms can be considered, alone or with other organisms, as successful against somewhat less than a hundred species of pests. The summarized list follows:

PARASITES			
Hymenoptera	63	Bacteria	1
Diptera	7	Fungi	1
Viruses	4		
PREDATORS			
Coleoptera	19	Mollusca	1
Hemiptera	4	Reptilia	1
Hymenoptera	4	Amphibia	1
Neuroptera	2	Aves	1
Acarina	4	Pisces	2 +



Nearly three-fourths of these are parasites, belonging to Hymenoptera, Diptera and microorganisms. Nearly all of the beneficial parasitic insects are Hymenoptera. The success of insect parasites to control pests is associated with their ability to seek out and locate their hosts even when scarce or widely separated. About one-third of the selections listed are the result of the activities of predators, which shows the importance of predatory species in the biological control complex, a fact not generally realized by entomologists. However, nearly all of the successful insect predators have preyed on homopterous insects. This is probably associated with the need for these predators to have a large and ready food supply to complete development of the immature stages.

Among the insects one successful parasite and one successful predator have been replaced by superior parasites. The same predator, *C. montrouzieri*, has been partially replaced in another instance by other predators and a parasite. Two insect parasites and two vertebrate predators have ceased to control hosts after commercial effectiveness for a number of years.

It is evident that most of the selections of successful biological control occur on oceanic islands or ecological islands, the vast majority of the examples being in such areas. The ecological islands include California, Washington, Italy, and portions of Australia and Mexico, which have areas well isolated by natural barriers. California and the Hawaiian Islands, an ecological and an oceanic island, are conspicuous for the large number of successes. It is no longer necessary to use insecticides in the sugarcane fields of Hawaii for any pest (Pemberton 1953, correspondence). A portion of the credit must go to the workers involved as well as to the environment. Successful control has been attained in several extensive continental areas in the United States, Canada, Africa and China, although distribution of the food plants of the pests serves as a barrier in some instances.

It is noteworthy that some of the pests live in relatively inaccessible places, as soil, and have habits that seem less favorable to the attacks of enemy organisms, yet the attacks of these beneficial species seem to be almost equally successful as enemies of exposed forms. This is especially encouraging, for it demonstrates the feasibility of attempting parasite and predator control of pests living in varied, hidden, and unusual habitats.

In nearly all of the examples listed, species other than those listed attack the pests, but the principal parasites and predators are given, and in most cases they are not appreciably aided by the species omitted. It is notable that the successful examples have in most instances been brought about by one parasite or predator.



# Biological Control in Germany

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## ABSTRACT

During recent years efforts have been intensified in the German Federal Republic to use biological control methods in combating pest insects of cultivated plants. It was possible through financial assistance given by the Federal Department of Agriculture and by the Deutsche Forschungsgemeinschaft to laboratories of the provinces (Laender) to commence work in the following fields of research: ecological communities (biocoenoses); population dynamics; protection of native beneficial insects when applying chemical control methods (through concentration of the effect of insecticides in space and time, and through development of more selective chemicals); re-colonization of native beneficial organisms which were greatly reduced by influences of men.

In the Laboratory of Biological Control set up in 1953 (Biologische Bundesanstalt, Darmstadt) in addition to fundamental research on population dynamics mainly such projects are dealt with which need special equipment and team work of experts. The point of main effort, presently, is basic and applied research on pathogenic microorganisms for biological control of pest insects. Further plans include importation and mass-rearing of entomophagous organisms to combat pest animals and weeds from abroad. One project of this type is, at the moment, handled by the Landesanstalt fuer Pflanzenschutz (Stuttgart): Mass-rearing of *Prospaltella perniciosi* (Tower) to control the San José scale (*Quadraspidotus perniciosus* (Comst.)). The review gives examples of the current work and first results.

Biological control work in Germany is not fully developed. It has, however, some history of successful research and application before the last war. The long tradition of bird and ant protection and colonization might be mentioned here, and even one example of establishment and economic importance of an introduced parasite, *Aphelinus mali* (Hald.), to control an imported pest insect, the apple woolly aphid, *Eriosoma lanigerum* (Hausm.). In the years immediately after the second world war, interest in biological control work in Germany was low as it was of primary importance to get quick results in protecting each year's harvest. The newly invented organic synthetic insecticides seemed to be ideal for this purpose. More recently, however, it appeared desirable to develop not only chemical but also biological methods for pest control and in 1952 the Department of Agriculture of the German Federal Republic decided to further biological control projects and associated research.

The main reasons for this new and enlarged trend in pest control were: The toxic effect of many pesticides on men and domestic animals; the appearance of pests resistant against chemicals; the risky consequences of the intensive use of pesticides to the biocoenosis; and finally, the continuous introduction of new pest insects from abroad.

Fig. 1 indicates possibilities of using native and imported beneficial organisms to combat pests and weeds. The left part of the figure deals with native and the right with foreign or imported organisms. The expressions "native" and "endemic" as well as "foreign" and "imported" are used here as ecological terms whereby the ability of newly introduced species to survive in the new biocoenosis is a self-evident premise.

The squares symbolize the type of application of beneficial organisms, the circles pests and weeds. The arrows show where introduced organisms might also be of use against native pests, and vice versa. The width of the arrows indicates the results reached so far by the different types of application. The marginal pattern of the squares indicates whether these projects are, in principle, handled by laboratories of the Laender (striped) or by Federal laboratories (dotted). I will describe briefly the organization of this work and some of the projects; more details are given in a recent review article (Franz, 1956).

The idea underlying the distribution of the projects is as follows: When a great deal of special equipment and a team of experts is necessary, the work is done by the

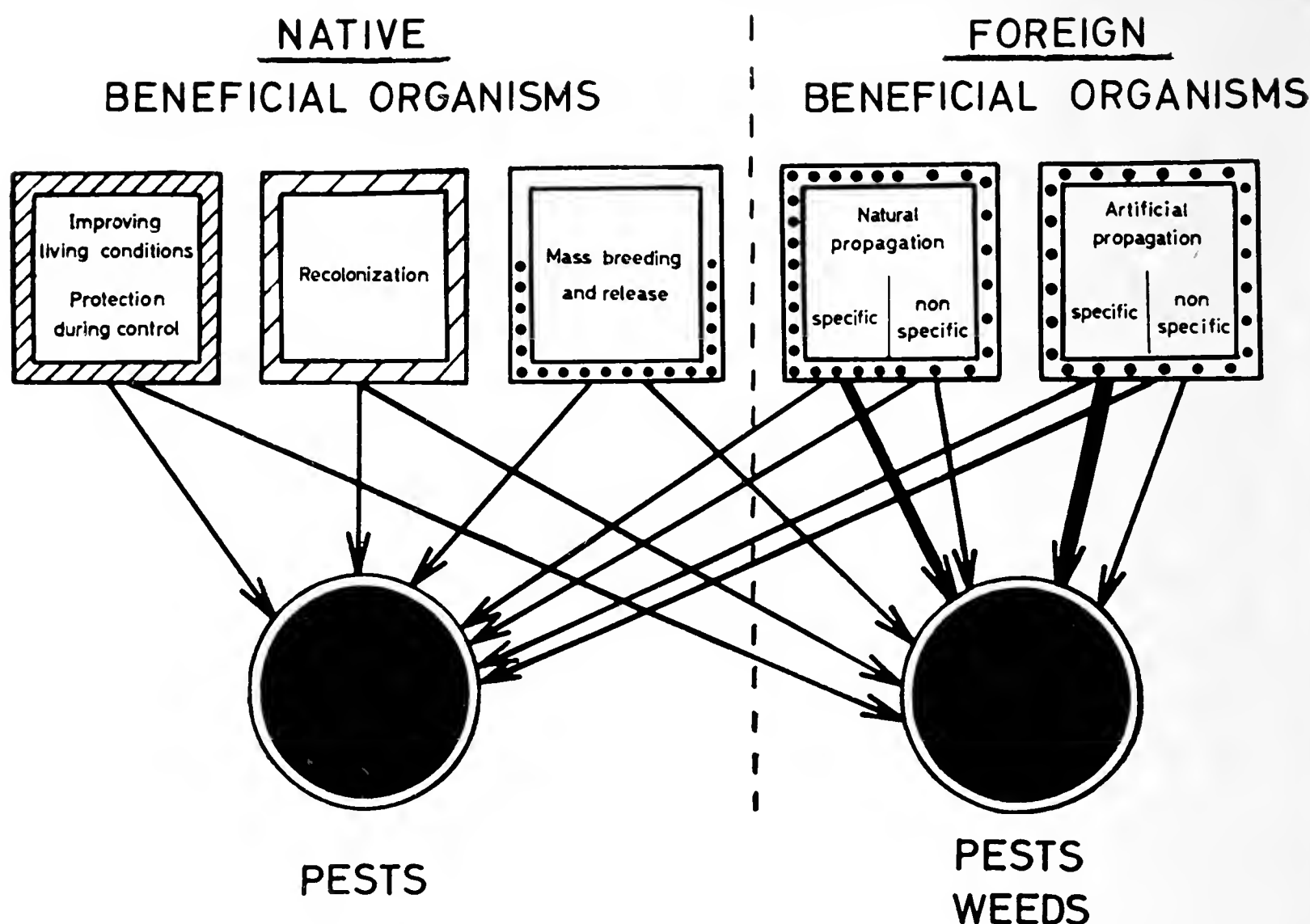


Fig. 1. Types of biological control. Left: Native organisms; right: Foreign organisms. Squares and arrows are symbols for the application of beneficial organisms, circles for pest organisms. For further explanation, see text.

Laboratory of Biological Control (Institut fuer biologische Schaedlingsbekaempfung), Biologische Bundesanstalt fuer Land-und Forstwirtschaft, Darmstadt, which was founded in 1953. As a federal institute, it is able to handle projects in different parts of West Germany. If the project is more regional and no special equipment is needed, it is assigned to provincial laboratories such as university laboratories, plant protection offices, and bird protection stations. These laboratories are usually subsidized by the Federal Government for this purpose.

The work of such provincial laboratories will be reviewed first. The following four fields of activity are primarily considered (see also Fig. 1):—

1. Specific protection of beneficial organisms during chemical or mechanical control of pests by:
  - a) Application of more or less specific pesticides or techniques of control;
  - b) Concentration of chemical or mechanical control treatments in space, for instance application of insecticide rings on trees instead of total spraying of forests;
  - c) Timing of control treatments so that beneficial organisms suffer the least possible damage; for instance application of insecticides that have no residual effects before the appearance of an important parasite;
  - d) Replacing of routine chemical control methods with modified treatments against individual pests only, and using minimum dosages; it is also hoped in this way to postpone appearance of strains resistant against insecticides.

All projects in these categories are concerned with the specific protection of beneficial insects. They usually start with the study of the natural control factors of the pest and lead to experiments of a combination of biological and chemical control. Of this type are, for instance, studies on forest insects like *Tortrix viridana* L. on oak, *Coleophora laricella* Hbn. on larch, *Choristo-*

*neura murinana* (Hbn.) on fir, and several sawflies on coniferous trees. The influence of various pesticides upon fruit and crop pests is investigated following the example of Pickett, Massee, and their co-workers. The following projects might be mentioned: Red spiders (*Metatetranychus ulmi* Koch and other species), the butterflies *Aporia crataegi* L., *Pieris rapae* (L.) and *P. brassicae* (L.); Carabidae and other predators in the fields; and the influence of chemical control upon the biocenosis of potato, oil seed, and sugar beet fields.

2. A further group of studies carried out by provincial laboratories is concerned with the recolonization of native, beneficial organisms that have suffered from human activities. For instance: Investigation and propagation of the red forest ant (*Formica rufa*); and experiments of seven West German bird protection stations to increase the population density of insectivorous birds. These studies are usually carried out in actual or prospective outbreak areas of pest insects with the object of finding the net result of predation by ants and birds on the population dynamics of insects.

The following types of biological control projects handled by provincial laboratories are mostly still in the exploratory phase:

3. Cultivation of special plants to improve living conditions for beneficial organisms, e.g., food plants for parasitic insects and their alternate hosts.
4. Use of domestic animals in biological control.

The so-called classical method of biological control, the importation of beneficial organisms to control introduced pests and weeds has been little used in Germany to date. One example was already mentioned: The control of the apple woolly aphid by the aphelinid parasite imported about thirty years ago. After some success in warmer parts of Germany, its efficiency decreased recently owing to the increasing application of contact insecticides in apple orchards. Studies are now being started to devise a modified spray program that is not harmful to *Aphelinus mali*.

A new project of mass rearing and colonization of an imported parasite *Prospaltella perniciosi* (Tower) to control the San José Scale, *Quadraspidiotus perniciosus* (Comst.), is in progress at the Landesanstalt fuer Pflanzenschutz, Stuttgart. The parasite has been released since 1954 and it hibernated in the field successfully, but economic control is not yet achieved. Further projects of this type will come up with the increasing menace of new importations and immigrations of pest insects from abroad like *Hyphantria cunea* (Drury) and the Japanese beetle.

Mass rearing of beneficial insects requires expensive equipment and is of more than regional interest. It is therefore planned to handle such projects in future mostly in federal laboratories. Whereas the preparative studies on the physiology and behaviour of beneficial insects will be treated by the Institut fuer physiologische Zoologie, Biologische Bundesanstalt fuer Land-und Forstwirtschaft, Berlin-Dahlem, the mass-rearing and colonization of entomophagous insects will be assigned to the Institut fuer biologische Schaedlingsbekaempfung, Darmstadt. Until the necessary insectaries are obtained, the work of the staff of the last mentioned biological control laboratory centers on the following main points of effort:—

1. Basic research on the population dynamics of insects with particular emphasis on efficiency of entomophagous insects and of epizootics. In this connection studies on the following pest insects might be mentioned: Balsam woolly aphid *Adelges (Dreyfusia) piceae* (Ratz.), fir shoot moth *Choristoneura murinana* (Hbn.), and maybeetle *Melolontha* sp. Both the last two topics belong partly also to the second group of studies.

2. Insect pathology comprising fundamental research on the nature of causative agents, and on histopathology, as well as application of disease organisms in practical biological control. The general studies are, for instance, on latency of virus diseases, diagnosis and staining methods of polyhedra and granula, and the use of fluorescent microscopy and serology for diagnosis and observation of pathological reactions of the cells. The more practical tasks are a survey of insect diseases occurring in Germany and tests to find out if some of them are important as natural control factors and



suitable for artificial infections of natural populations. For the first time in Europe a virus disease has been successfully applied in biological pest control: The polyhedrosis of the European pine sawfly *Neodiprion sertifer* (Geoffr.) proved to be effective after artificial spread in the enzootic area of host and disease. This experiment supplemented the results of Canadian research workers who infected disease-free populations of the same sawfly with virus imported from Europe. Furthermore, it was found that the polyhedra of this species remain infectious after passage through the intestinal canal of a predatory insect and of a bird.

In conclusion, it might be mentioned that the Darmstadt laboratory of biological control is also supposed to develop the international relations which are of particular importance in this field of research. Efforts in biological control in Germany should not be considered as isolated. They conform closely with the work in other European countries. This common interest initiated the formation of the Commission Internationale de Lutte Biologique (CILB). The co-operation of the Darmstadt laboratory with the Commonwealth Institute of Biological Control and, with the University of California and Science Service, Department of Agriculture, Canada, is close and successful. Through the kind assistance given by many colleagues of Science Service it was possible for me to study some problems here in Canada that might hardly be understood without comparison of the situation in the New and the Old World.

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# Biological Control of Insect and Plant Pests in the Trust Territory and Guam

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## ABSTRACT

The Trust Territory of the Pacific Islands comprises the Micronesian Island groups known as the Carolines, Marianas, and Marshalls, with the exception of Guam. In 1947 the Pacific Science Board of the National Academy of Sciences, National Research Council appointed the Invertebrate Consultants Committee for the Pacific to plan and direct the entomological work in these islands. One of the main objectives of this Committee has been the introduction into the islands of beneficial insects to combat insect pests and weeds, many of which are of foreign origin. This has been accomplished by sending explorers to foreign areas to collect the beneficial forms and ship them to the islands, and by obtaining them through the courtesy of various agencies in the United States, Hawaii, Mexico, Philippines, India, Java, and Fiji. Financial aid to carry on the investigations has been supplied primarily by grants from the Office of Naval Research of the Department of the Navy.

During the eight years that this Committee has been functioning, 43 beneficial insects and 1 insect disease have been introduced to combat over 20 insect pests and 1 weed. Of these, 12 are known to have become established, and several of the important pests are now being controlled by these beneficial insects. No doubt a careful survey would reveal the establishment of other introduced species.

### COCONUT RHINOCEROS BEETLE, *Oryctes rhinoceros* (L.)

The coconut rhinoceros beetle, a common pest of palms throughout southeast Asia, was first observed by the natives in the Palau group of the Western Carolines about 1942 (Gardner, 1953). It increased rapidly and soon became a serious menace to the coconut palm, which is important to the economy of the islands. The adult beetles tunnel into the crown of the palm, where they feed on the succulent tissue and sap of the inner leaves. Severe feeding may kill the trees.

From 1947 to 1951 explorers were sent to East Africa and southeast Asia in search of natural enemies of this beetle and related species. Adults of the scoliid, *Scolia ruficornis* (F.) were collected on Zanzibar Island, and a number of consignments were sent to the Palau Islands (Gardner 1953, Pemberton 1954). This parasite was found to be established in 1953, and is now common on the islands of Koror and Babelthuap. It is expected to bring about an appreciable reduction of the beetle in the near future.

In 1948 another scoliid, *Scolia patricialis* (Burm.) subspecies *plebeja* (Gribodo), was collected in Malaya and sent to the Palaus, where it was liberated on Koror (Gardner 1953). There is yet no indication that this parasite has become established.

Other liberations of beneficial insects in the Palau Islands to combat this beetle consisted of the larva-feeding histereid beetles *Placodes ebeninus* (Lew.) from Tanga, Tanganyika, and *Pachylister chinensis* (Queng.) from Samoa (Pemberton 1954). There is no evidence that these predators have become established. *Leinota* sp., which was introduced into the Palaus from Trinidad to feed on larvae of the banana root borer, may also attack the larvae of the coconut rhinoceros beetle.

The pathogen, *Bacillus popilliae* (Dutky), effective in reducing Japanese beetle infestations in the United States, was tested on *Oryctes* grubs in the Palau Islands, but the results are inconclusive (Steinhaus 1951).

### MARIANA COCONUT BEETLE, *Brontispa mariana* (Spaeth)

The Mariana coconut beetle is a serious pest of the coconut palm on several of the Mariana Islands. This hispid is a native of the Caroline Islands, but does not seem to be a pest of any great importance in that group. The larvae and adults feed

between the unfolded leaflets of the palm crown. Heavy infestations kill the leaves, and if feeding is prolonged the tree may die. Esaki (1940), who first observed this beetle on Saipan in 1931, states that in 1935 and 1936 about 70 percent of the coconut trees on the island were burned in an attempt to check the damage caused by this insect. The native earwig, *Chelisoches morio* (F.), feeds on larvae of the beetle, but is of little value in controlling the pest.

In the fall of 1947 an explorer was sent to the Philippines, Malaya, and Java in search of the natural enemies of the genus *Brontispa*. Although *Brontispa* was found in the Philippines, no natural enemies of importance were encountered there. In Malaya and Java the larval-pupal parasite, *Tetrastichus brontispae* (Ferr.), and the egg parasite, *Haeckeliana brontispae* (Ferr.), were found, and early in 1948 four consignments were sent to the Trust Territory and several thousand adults were liberated on Saipan and nearby Rota (Lange 1953). Observations later that year revealed that *Tetrastichus* was well established and spreading on both islands, with larval and pupal parasitization running as high as 89 percent in some locations (Doutt 1950). Observations on Saipan in 1954 indicated that the beetle was well controlled by this parasite. There is no evidence that *Haeckeliana* has become established.

#### RED COCONUT SCALE, *Furcaspis oceanica* (Ldgr.)

The red coconut scale appears to be native to the Pacific islands and occurs in most areas where the coconut palm is grown. On Saipan it is second to the Mariana coconut beetle as a pest of coconut. This purplish-red scale feeds along the midribs of the fronds, giving the foliage a reddish appearance.

Investigations in the Western Carolines in 1948 (Doutt 1950a) revealed that the scale was controlled by the encyrtid *Anabrolepis oceanica* (Doutt). Therefore, in the fall of that year a consignment of this parasite was forwarded to Saipan for release. It is doubtful whether it has become established in the Marianas.

#### BANANA ROOT BORER, *Cosmopolites sordidus* (Germ.)

The banana root borer occurs throughout Micronesia. Although present on Guam for many years, it was not observed on Saipan until 1939. The larvae bore into the trunk of the banana plant above and below the ground, causing fiber injury with resultant decay.

In July 1947 the histerid beetle *Plaesius javanus* (Erich.), which had been introduced into Fiji from Java in 1914 and proved to be of considerable value in holding down the borer, was received from Fiji and released on Guam (Bryan 1949). It was reported established on the island in 1949.

Over 100 adults of the hydrophilid beetle, *Dactylosternum hydrophiloides* (W. S. M'Leay), were collected in Malaya in 1948, forwarded to the Palaus, and liberated on the island of Koror. It is not known whether this beetle has become established.

In March 1953 a species of *Leinota* was received from Trinidad, where it was found feeding on larvae of the banana root borer, and released on Guam and on several islands of the Palaus (Pemberton 1954). It is not known whether this predator has become established.

#### ORIENTAL FRUIT FLY, *Dacus dorsalis* (Hendel)

Although the oriental fruit fly had been recorded on Saipan in 1924 (Esaki 1940), it was not found on Guam until 1947 (Maehler 1948). This insect of Asiatic origin is a serious pest of various fruits and vegetables.

Several consignments of parasites were obtained from Hawaii in 1950 and 1952 and released on Guam and Saipan. They consisted of the opiines, *Opius compensans* (Silv.), *O. formosanus* (Full.), *O. incisi* (Silv.), *O. longicaudatus* (Ashm.), and *O. persulcatus* (Silv.), and the two chalcids, *Dirhinus giffardii* (Silv.) and *Syntomosphyrum indicum* (Silv.). These parasites, mostly from southeast Asia, had been introduced into Hawaii several years before to combat the oriental fruit fly. Judging from their effectiveness in combating this fruit fly in Hawaii, it is believed that similar results will be obtained on Guam and Saipan.

**MELON FLY, *Dacus cucurbitae* (Coq.)**

The melon fly, a serious pest of various cucurbits and some fruits, has been known to occur in the Mariana Islands for a number of years, and on Guam since 1936. To combat this pest the braconid parasites, *Opius fletcheri* (Silv.) and *O. watersi* (Full.) were introduced into Guam from Hawaii in 1950 and 1952 (Pemberton 1954). There is no indication that they have become established.

**SPINY BLACKFLY, *Aleurocanthus spiniferus* (Quaint.)**

The spiny blackfly was recorded on Guam in 1951 (Peterson 1955a) and is thought to have gained entrance on introduced citrus or rose plants. This aleyrodid of Asiatic origin soon became the most serious pest of citrus on the island. Heavily infested trees lose their vitality, and continued feeding on the leaves eventually kills them.

In 1952 nearly 60,000 parasites, representing the species *Amitus hesperidum* (Silv.), *Eretmocerus serius* (Silv.), *Prospaltella smithi* (Silv.), *P. clypealis* (Silv.), and *P. opulenta* (Silv.), were received from Mexico and released on Guam. These parasites had been introduced into Mexico from India several years earlier by the United States Department of Agriculture to combat the closely related citrus blackfly *Aleurocanthus woglumi* (Ashm.). *A. hesperidum*, *E. serius*, and *P. smithi* became established, and by the fall of 1953 from 75 to 90 percent of all districts on the island infested with this pest were practically clean.

**EGYPTIAN MEALYBUG, *Icerya aegyptiaca* (Dougl.)**

The Egyptian mealybug, probably of oriental origin, occurs throughout the Trust Territory, and on some islands is a serious pest of avocado, banana, breadfruit, citrus, and certain ornamentals. Investigations in 1947 revealed that it was held in check in the Mariana Islands by the predator *Rodolia pumila* (Weise) and in the Palau Islands by a closely related coccinellid.

From 1947 to 1949 *R. pumila* was collected in areas of its abundance in the Marianas and released on Truk, Ulithi, Kwajalein, and other islands of the Carolines where the mealybug was abundant. The coccinellid became established on each island, with satisfactory results in checking this mealybug. In 1953 colonies of the species in the Palaus were liberated on Pingelap Island in the Eastern Carolines and on Jaluit Atoll, Kwajalein, Eru, and Lae Atoll in the Marshall Islands (Bryan 1949, Pemberton 1954).

In 1948 several consignments of a species of *Rodolia* known to attack this mealybug in India were received from that country and released on Guam and the Majuro Atoll in the Marshalls (Pemberton 1954). A search for this predator on Majuro in 1953 did not reveal its presence, nor does it seem to have become established on Guam.

**TARO LEAFHOPPER, *Tarophagus proserpina* (Kirk.)**

A common pest of taro, an important food throughout Micronesia, is the taro leafhopper. It was first recorded on Guam in 1924 and is known to occur on most of the islands of the Territory. The Malay Archipelago is probably its native home.

Several years ago the egg-feeding mirid bug, *Cyrtorhinus fulvus* (Knight), was introduced into Hawaii from the Philippines to combat this leafhopper and soon controlled it there. In 1947 a consignment of the predator was received from Hawaii and released on Guam, where it became established and brought the leafhopper under control (Pemberton 1954). Later, adults were collected on Guam and sent to Ponape with good results.

**PHILIPPINE LADYBIRD BEETLE, *Epilachna philippinensis* (Dke.)**

In 1948 the Philippine ladybird beetle was observed on Guam (Maehler 1948), and later it was found on nearby Saipan, Tinian, and Rota Islands. Within a very short time it became a serious pest of various solanaceous vegetable crops.

Several shipments of adult *Paradexodes epilachnae* (Ald.), a tachinid parasite of the closely related coccinellid, *Epilachna varivestris* (Muls.), in Mexico, were received from that country in 1950 and 1952 and liberated on Guam. There is no evidence that it has become established on the island.



Early in 1954 a small number of *philippinensis* pupae parasitized with the eulophid *Pediobius epilachnae* (Rohw.) were received from the Philippines. Adult parasites emerging from this material were used in laboratory propagation, and during the year were released at 12 locations on Guam. In 1955 it was reported that the parasite had become established and was very effective in controlling the beetle throughout the island (Peterson 1955c).

#### EUROPEAN CORN BORER, *Pyrausta nubilalis* (Hbn.)

The European corn borer was first recorded on Guam in 1911, under the synonymous name *Pyrausta vastatrix* (Schultze) (Fullaway 1912), and by 1920 it was reported damaging 50 per cent of the corn crop on some parts of the island. It is also known to occur on Saipan and the Palau Islands.

Attempts made in 1926 and 1928 to introduce several parasites of the borer into Guam from the United States were unsuccessful (Vanderburg 1928, 1930). In 1931 a strain of the tachinid, *Lydella grisescens* (R.D.), was received from Japan and released on the island (Vanderburg 1933). It became established and rapidly reduced the borer population (Swezey 1940). However, for some unknown reason *Lydella* gradually disappeared, and by 1951 the borer again was causing serious damage to corn.

In 1952 and 1954 consignments of field-collected parasitized corn borer larvae were received from the United States, from which the following parasites were reared and liberated: *L. grisescens*, *Chelonus annulipes* (Wesm.), *Horogenes punctorius* (Roman), and *Macrocentrus gifuensis* (Ashm.). There is yet no evidence that *Lydella* or the other parasites have become established (Peterson 1955b).

Early this year a similar consignment was received from the United States and released on Saipan.

#### CHINESE ROSE BEETLE, *Adoretus sinicus* (Burm.)

The Chinese rose beetle, a native of the Orient, was found on Guam in 1949, and later was recorded from several other nearby islands in the Marianas. It is presumed to have been introduced from Hawaii, where it became established many years ago. It soon became one of the most serious pests on Guam, the adults defoliating a wide variety of economic food plants, ornamental trees, shrubs, and vines.

In 1950 and 1951 several consignments of the scoliid wasp *Campsomeris marginella modesta* (Sm.), which was introduced into Hawaii from the Philippines about 30 years ago, were liberated on Guam (Pemberton 1954). Although this parasite has become established, it is too early to evaluate its effectiveness.

#### FALSE BLACK WIDOW SPIDER, *Latrodectus geometricus* (Koch)

The poisonous false black widow spider is known to occur on several islands in the Territory. On Kwajalein it was found to be abundant in residential buildings, and in 1950 a consignment of the eurytomid wasp, *Eurytoma latrodecti* (Full.), was received from Hawaii and released (Pemberton 1954). Eleven months later it was found established.

#### LANTANA WEED, *Lantana camara* (L.)

*Lantana camara*, a native shrub of Mexico, has become established on many islands in the Pacific. On Ponape in the Eastern Carolines it has become particularly troublesome, especially in areas where the coconut palm is cultivated.

In 1948 and 1949 the tingitid, *Teleonemia scrupulosa* (Stål.), the tortricid, *Epinotia lantana* (Busck); the plume moth, *Platyptilia pussillidactyla* (Walker); and the seed fly, *Ophiomyia lantanae* (Froggatt) were received from Hawaii and released to combat this weed (Bryan 1949). *Teleonemia* and *Epinotia* have become established and are exerting some control.

#### MISCELLANEOUS INTRODUCTIONS

The following beneficial insects have been recently introduced into Guam from Hawaii: The parasitic ampulicid wasp, *Ampulex compressa* (F.), to combat cockroaches; the dung-feeding scarabaeid beetle, *Copris incertus* var. *prociduus* (Say), to feed on



larvae of *Musca domestica vicina* (Macq.), *M. sorbens* (Wied.), and other filth flies; the coccinellids, *Orcus chalybeus* (Boisd.) and *Platyomus lividigaster* (Muls.), to feed on various species of scales and aphids which are abundant on the island; and the non-blood-sucking predaceous mosquitoes, *Toxorhynchites brevipalpis* (Theob.) and *T. splendens* (Wied.), to combat the mosquitoes *Aedes albopictus* (Skuse) and *A. pandani* (Stone) (Pemberton 1954). It is too early to determine whether these beneficial insects have become established or to evaluate their effectiveness.

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# Biological Control in Poland

By HENRYK SANDNER

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It is an undoubted fact that Poland is not one of the privileged countries from the point of view of the possibility of effective biological control of destructive insects. Her geographical situation and climate do not afford favourable conditions for the application of these methods. It should be emphasized, however, that what are termed "good" conditions for applying biological methods of control are as a rule connected with a far greater degree of gravity of plant protection problems than is met with in Poland. It must also be added that the above opinion is the result of present-day Polish thought on the possibilities of biological methods. According to these ideas, a greater degree of success can only be obtained by the introduction of entomophagous insects. This enables us to view the problem of utilising local entomophagous insects in an entirely different light to-day.

The pioneer of biological methods of control in Poland was Mokrzecki. As early as the World War I period, during his stay in the Crimea, he carried out tests on the control of the codling moth by the use of *Trichogramma semblidis* Aur.

In the '20s, as a result of Mokrzecki's contact with Howard, two stations were established in Poland for the purpose of collecting parasites of gypsy moth for export to the USA.

The greatest single action in biological control in Poland was breeding and distribution of the *Aphelinus mali* Hald. in the '30s. This action has not as yet been renewed since the war.

In the years immediately preceding the War, Boczkowska carried out, but without great success, tests of microbiological control of the *Piesma quadrata* Fieb. using the fungus *Beauveria* sp.

"Tachinaria" were also used in silviculture but without much success.

To the above can also be added the action to protect beneficial birds in Poland, which enjoyed varying success and of which Sokolowski has been the patron for many years.

This brings to a close above modest survey of practical actions to implement biological control of pests carried out so far in Poland.

I shall now turn to a discussion of the prospects for this method in the immediate future in Poland.

The actual possibilities of applying biological methods in Poland apart from the protection of beneficial birds are not great. They are limited, in effect, to the use of three entomophagous insects: *Aphelinus mali*, *Trichogramma* sp. and *Apanteles* sp. To these may be added certain instructions regarding the protection of certain beneficial forms (for instance lady beetles). Further attempts to establish "tachinaria" are also desirable. Certain actions should be planned now, to be put into effect before long.

The question arises as to whether, in view of the very slight possibilities existent it is worth while making great efforts to initiate or to set on a proper footing action for biological control. Undoubtedly taking plant protection action as a whole the effect of these biological methods will be of little evidence but they are nevertheless of real material advantage. Even more important they blaze the trail for the idea itself of biological control of destructive insects, popularise it in the localities concerned and enable the conviction, that chemistry is not the only effective weapon in insect control to take hold.

## APHELINUS MALI

*Aphelinus mali* was brought to Europe and breeding begun in 1920. It was introduced into Poland several times since 1928. It may also be presumed that *A. mali* reached Poland by natural means from the west and south of Europe. When a search was carried out in connection with a consignment of *A. mali* sent from England it was found that this parasite had already domiciled itself in many places. It was, at the time, difficult to find out if the previous consignment of *A. mali* or possibly accidental

introduction had brought this about or whether it was the result of active distribution of this species during the years 1935-1939.

Several plant protection stations bred *A. mali* and supplied districts with them. In the post-war years the problem of control of the woolly apple aphid was first of all shelved for action at a later date. On the one hand new and more important problems arose, and on the other the severe winters of 1939/40 and 1940/41 greatly limited the occurrence of this insect pest in Poland. Today, however, the woolly apple aphid has become a common and destructive orchard pest. According to various unpublished data, *A. mali* occurs in practically all parts of Poland. On these grounds it may be assumed that this parasite has acclimatised itself here and plays a certain part in the natural reduction of the numbers of the woolly apple aphid. We do not, however, know exactly what this part is. We do not know the extent or the frequency of occurrence of *A. mali*. In order to arrive at a clear idea of the situation, it is essential that the necessary research work should be carried out. Judging by the experience of the other countries, however it can be stated that the breeding and distribution of this parasite or at the very least the provision of suitable hibernation conditions for it, is essential.

The clearly-formulated tasks with regard to the active utilisation of the *A. mali* in Poland are as follows:

1. The organization of an action to collect, in the late autumn, branches infested by woolly apple aphid which *A. mali* has dominated. The branches should be kept in a cool place during the winter, and in the spring should be taken to orchards where pests have been controlled and placed on the apple trees.

2. The organization of 1 or 2 permanent breeding stations for the *A. mali*. In this way a reserve could be built up to be available for use in the summer, especially in the central and northern regions of Poland, where as may be presumed the natural activity of *A. mali* is less effective on account of unfavourable atmospheric conditions.

3. The planning and execution of research work on the numbers, extent and part played by *A. mali* in Poland. This is essential to the correct planning and putting into effect an action to utilise the *A. mali*.

### TRICHOGRAMMA SP.

Parasites of the eggs of insects arouse, by their very nature, the greatest interest in us, since they attack the insects at the most suitable time: not only before they are capable of reproduction but before they begin their destructive activities. The egg parasite most popular for many years now amongst scientific workers on biological control methods is *Trichogramma* sp.

The first successful experiments on the utilisation of *Trichogramma* were carried out in 1912 in Tashkent and in the following years in the Crimea. Mokrzecki made a valuable contribution to this work. The turning point in the development of this method was the working out in 1926 by Flanders of the method of breeding *Trichogramma*. Since that time particularly in the United States and the Soviet Union the breeding of various species of *Trichogramma* sp. has been carried out on a large scale.

The presentation of the problem of *Trichogramma* as a whole is at present rendered easier by the fact that this question was dealt with, as regards the position in Ukraine, by Kowalewa (1954), and as regards the position in Central Europe, by Mayer (1955).

In the Ukraine *Trichogramma* has proved itself most effective in the control of various owl moths. Working methods for the breeding and distribution of *Trichogramma* have not yet been drawn up in their final form. Kowalewa affirms that many mistakes have been made up to the present (i.e. 1954). Amongst these mistakes is the application of too large doses of the parasite (up to 300,000 per hectare). Further, stable humidity and temperature conditions have been maintained during breeding, without taking into consideration the varying climatic conditions of the areas of

distribution. Degeneration as a result of continual mass breeding has not been taken into account. This degeneration appears in the shortened life-span of the fully grown forms (which is shortened to 4-5 days) which decreases the chances of attacking the entire number of eggs. Since 1944 work has been going on to correct certain mistakes. Among others may be cited the introduction of re-invigoration of the generations by material collected from the distribution areas, which increases the life-span almost two fold (to 10 days). In addition — from the middle of April to the end of Summer — breeding is carried out in natural conditions in the open air. In the winter the insects are subjected to the action of varying temperatures which are lowered at night. These methods have markedly increased the effectiveness of *Trichogramma*.

Work has been recently carried out in the Ukraine on the choice of the most suitable host under artificial breeding condition. The problem of "dosage" has been partly solved by Mayer, who demonstrated that doses of over 100,000 per hectare decrease effectiveness, since the same eggs are then attacked several times and degeneration ensues. The optimum number is considerably less — about 20,000 females per hectare. A more precise method of distribution of the infected eggs has also been worked out, which is of great importance, since *Trichogramma* is capable of a limited flight only, and does not usually exceed 20 m. during the entire life. I have referred to these matters in order to emphasize that we shall not find 100% certain prescriptions for methods of utilizing *Trichogramma* straight away. The problem of working out methods suited to our country arises, both in the case of the control of cutworm moths and other agricultural destructive insects, and for control of the codling moth.

According to information given by Mayer, results of research work in the beginning (Hase 1924) were not encouraging. One of the causes was the use of the American species *T. minutum* Ril. which was not adapted to Central European conditions. Mayer's analysis may also be of value to us. In Central European conditions two species are concerned: *T. semblidis* Aur. and *T. cacoeciae* March. in various forms. Ferrier's last works serves as a guide in these matters. Physiological differences between various species and forms are considerable, which is of course of importance when making use of them in given areas.

Recent research in Germany was concentrated on *T. cacoeciae*, as being the most suitable species from many points of view. The "flood method" is used, that is the method accepted in the United States by Flanders and also applied in the Soviet Union. As regards certain failures, Mayer believes the cause to be a too superficial estimation of the relation of parasite to host. The question of the power of attraction of various species in a given biocenosis is often under-estimated, and this is view of large polyphagism may be of great importance. Although Quednau's latest researches (1955) show that there is no question of pantophagism with this genus *Trichogramma*, yet the whole of so-called entirely hosts and ecological unbounding hosts is sufficiently great to make the problem of power of attraction play a practical part.

Final definition of the method in detail must therefore be laid down in every case for the specified biocenotic conditions.

Five generations of the *T. cacoeciae* occur in our country annually. The groups of hosts change in relation to this under natural conditions.

It would appear that under the conditions existent in our country, *Trichogramma* could be used in the cutworm moths control and that the possibilities of its use in control of the codling moth should be investigated. In view of the relatively high flight capability (up to 20 m.) every 5th row in an orchard could be so treated, allowing 1000 per tree. This should be done every year. Calculation of the cost compared with the cost of chemical control, is very small. An additional effect of this treatment is the infection of the eggs of certain other insects.

According to data supplied by Telenga (1955) the phenomenon of negative coincidence occurs most frequently in relations between *Trichogramma evanescens* and *Agrotis segetum*. Human intervention is therefore most highly desirable. In field conditions the flight of *Trichogramma* comes within a radius of 50 m. which facilitates the carrying out of the action.



This is the sum total of information available on the practice of using *Trichogramma*, based on data from neighbouring countries. The following conclusions can be drawn with regard to conditions in Poland:

1. Methods of breeding and distribution of *Trichogramma* for purposes of cutworm moths control should be prepared as quickly as possible.
2. It is essential that 2 or 3 breeding stations should be organised for the time being.
3. The problem of *Trichogramma* in Poland, state of species, frequency of occurrence, distribution etc. should be determined as quickly as possible by research stations.
4. The possibilities of utilising *Trichogramma* for codling moth control should be investigated.

#### APANTELES SP.

The problem of *Apanteles* is generally well known because in text books and popular works it is given as an example of a typical beneficial form. Actually the case is slightly more complicated than it would appear, since six species of *Apanteles* occur in the cabbage worm. Undoubtedly *Apanteles glomeratus* L. plays the most important part.

Of 6-7 generations of *Apanteles*, the last 2-3 live in *Pieris brassicae* and *P. rapae* caterpillars. The first two generations attack *Aporia crataegi*. The possibility therefore exists of collecting the cocoons of *Apanteles* from the *A. crataegi* caterpillars and moving them to the infected cabbage. Several thousand cocoons per hectare are sufficient to cause infection of over 80% of the first generation of caterpillars (normally: 20-30%) and up to 95% of the second generation.

The question of the use of *Apanteles* in Poland in the practice of cabbage worm control is not however quite clear. It would appear that there are certain possibilities here and that the appropriate tests should be carried out. At the present time this question is the concern of scientific workers only, who should investigate the possibilities of collecting cocoons, and in the winter, the possibility of storing them until the cabbage worm appear on the young cabbages.

#### "TACHINARIA"

"Tachinaria" have been, and still are, set up from time to time in forests on a test basis. Trustworthy data are not available as to their economic rôle, since experiments are, as a rule, carried out under unsuitable conditions and are not properly controlled. No attempts have been made to set up "tachinaria" under field cultivation conditions, and it may be presumed that this would give very useful results. The following conclusion must therefore be reached: Suitably organised experiments should be carried out to ascertain the possibilities of biological control of agricultural destructive insects by the use of "tachinaria".

#### FUTURE PROSPECTS

The fact must be taken into consideration that before long the question of control of two destructive orchard insects will arise in Poland, namely the fall web-worm and the San José scale. It would appear that both these insects ought to compel us to investigate the possibilities of introducing certain species of parasites, by means of which it would be possible to prevent the development of these insects in Poland.

In summing up this short review of the present situation and the possibilities of biological control methods in Poland the necessity of setting up a responsible research centre to examine these methods must be emphasized. Such a centre should establish scientific contacts with similar centres in other countries.

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# Recent Work on Biological Control in the British West Indies

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After Dr. J. E. Myers and Mr. H. E. Box left the Caribbean area in the mid-1930's little further was done in the way of biological control in the British West Indies until 1946 when the Commonwealth Institute of Biological Control established a West Indian Station at the Imperial College of Tropical Agriculture, Trinidad.

During this interim period a certain amount of shipping around of predators and parasites from island to island did take place but not on an extensive scale, and a certain amount, in addition to his *Trichogramma* work, was carried out by Mr. R. W. E. Tucker in Barbados.

Various investigations and attempts to establish beneficial species are described below under the different crops involved, and mention made of investigations carried out in the British West Indies for other areas. Time will not permit discussion of previous work here and only a brief summary of these recent investigations can be given.

## SUGAR CANE

This is the most important economic crop in the British West Indies, and it has a number of important insect pests. The small moth-borers, *Diatraea* spp., are the most important.

*D. saccharalis* F. occurs throughout the area, *D. canella* Hmps. from St. Lucia southwards (excluding Barbados) through St. Vincent, Grenada, Trinidad and British Guiana (where it is now the most important species). *D. impersonatella* Wlk. is of lesser importance and is found in sugar cane principally in Trinidad, but to a lesser extent in British Guiana.

The work of Myers and Box (1931-1938) on parasites of *Diatraea* marked a definite phase in the biological control of this pest. The principal results were an economic control of *D. saccharalis* in Antigua and St. Kitts by *Lixophaga diatraeae* Tns. and in St. Lucia by *Megatonistylum minense* Tns. Introductions were made into some of the other islands but were unsuccessful.

More recently *Lixophaga* has been introduced into Montserrat, St. Vincent and Grenada with so far unknown results, and into Barbados and Trinidad without successful establishment. However, it has been rather unexpectedly successfully introduced in Dominica, where it might have been thought that the climate was too wet for it. *Metagonistylum* has been unsuccessfully tried in Grenada, St. Vincent, Barbados and Dominica.

Attempts to establish *Paratheresia claripalpis* Wulp in several areas have previously been unsuccessful but recently (1951) it has been established in Dominica where samples of *Diatraeae* larvae have given a parasitism of up to 85% and joint counts of bored cane have been lowered from about 30% to 5%.

A further recent advance in this field has been the development of a breeding technique for *Palpozenillia palpalis* Ald. which it had been previously impossible to breed in the laboratory. Liberations of this species against *D. canella* Hmps. (now *Eodiatraea centrella* (Mosch.) in Trinidad (and also against *Castnia licoides* (Boisd.), British Guiana, St. Lucia and St. Vincent have not resulted in establishment, but there are some grounds for supposing that a different strain of the parasite might be more successful.

It should of course be mentioned that in Barbados annual releases of millions of *Trichogramma* and *D. saccharalis* have continued during recent years.

In both Trinidad and British Guiana froghoppers of the genus *Aenolamia* cause serious and spectacular damage to cane, and other species which cause usually minor damage to cane are found in Grenada, Jamaica and British Honduras.

Extensive investigations in the past failed to produce successful biological control of *Aenolamia varia* Dist. in Trinidad. It has been suggested that chemical control

by means of modern insecticides which has been carried out in recent years is becoming increasingly difficult. Investigations have been made to determine if this could be due to the effect of the insecticides on parasite and predator populations. Interesting results have been obtained but they do not indicate on the whole that the natural enemies are being adversely affected.

Further work has been carried out utilising modern techniques on the possibility of using green muscardine, *Metarrhizium anisopliae* in the early part of the frog hopper season.

In 1952 there was a serious but localised outbreak of cane-fly in Jamaica. This continued in 1953 and investigations were carried out on the status of natural enemies. A number of parasites and predators were recorded, and subsequently material of additional parasites was sent from Trinidad—the egg parasite *Anagrus flaveolus* Water. and the dryinid *Pseudogonotopus* sp., either of which appears to have become established.

There is still a great deal to be done on the biological control of various cane pests in the British West Indies but very much more intensive investigation is necessary.

### COCONUTS

Coconut scale, *Aspidiotus destructor* Sign., is the most widespread serious pest, but it does not occur in Jamaica. A number of species of coccinellid prey on it, particularly in Trinidad, and have been used in its biological control elsewhere. Several of these species have been shipped in the past 10 years to other of the British West Indies without results except possibly in Barbados and St. Vincent. It is possible that a number of these coccinellids are very much more widespread among the Islands than has been supposed previously and that only infrequently are conditions such that small localised increases in population occur (e.g. *Azya orbiger* Muls. in Dominica and *Chilocorus cacti* L. in Barbados). A more intensive study of the local faunas is essential.

The coconut white-fly, *Aleurodicus cocois* Curt., has been a pest in Barbados, causing damage and disfigurement, both on coconuts and ornamental palms. Investigation showed that in Trinidad both coccinellid (Scymnine) predators, and a parasite *Prospaltella* n. sp., attacked this pest. These were successfully introduced into Barbados. *Prospaltella* became quickly established and gave satisfactory control of the white-fly.

In British Guiana there are two additional serious pests of coconuts—the defoliating larvae of *Brassolis sophorae* L. and the very large larvae of *Castnia daedalus* Cram. which bore in the crown and leaf bases and may kill the tree. Further investigations into the natural enemies of these two should be carried out.

### COCOA

In Trinidad and Grenada the cocoa beetle, *Steirastoma breve* Sulz., is a serious pest. Investigations of natural enemies were made in Trinidad for Grenada but no promising species were obtained.

The thrips, *Solenothrips rubrocinctus* Giard., is a widespread pest of cocoa and is particularly important where cocoa is growing under unfavourable conditions or exposed to excessive drying (by wind or strong sunlight). *Dasyscapus parvipennis* Gahan, an egg parasite, was successfully introduced into Trinidad, thence to Jamaica from West Africa, but, although well established, does not control or prevent outbreaks of thrips.

Mealybugs on cocoa (*Planococcus citri* Risso, etc.) are important as virus transmitters both in Trinidad and the Gold Coast. Parasites of these have been investigated in Trinidad, and several primaries sent to the Gold Coast for trial against cocoa mealybugs there.

### COFFEE

The coffee leaf-miner, *Leucoptera coffeella* Guer., is a serious pest of coffee in Dominica and Jamaica and a brief investigation of local parasites in Dominica was made with a view to the possible introduction of parasites from East Africa. Several parasite species attacked the leaf-miner but only two appeared to be of any major importance, *Elachertus* sp. and *Mirax insularis* Mues.

## CITRUS

Citrus weevils, *Prepodes* spp., in Jamaica and *Diaprepes* spp. in Dominica and St. Lucia are the principal citrus pests investigated. Several egg parasites occur and it is possible that an attempt will be made to introduce material from Dominica to Jamaica.

On the small island of Carriacou off Grenada *Orthezia insignis* Doug. is occasionally a serious pest on citrus. Here an egg parasite—a new species of Chamaemyid was found. The pest was studied in Trinidad and several coccinellids, a syrphid, *Bacca* sp., and an egg predator, *Gitona* sp., were found to attack *Orthezia*. These have been released in Carriacou (and Kenya) with as yet unknown results.

## RICE

Investigations of natural enemies of several species have been made: *Mormidea poecila* Dall., the padi bug, in Trinidad and Jamaica, and *Rupela* (*Scirpophaga*) *albinella* Craw. in British Guiana and Trinidad. From Trinidad a *Telenomus* sp. was shipped to Indonesia for trial against rice stem-borers there.

## COTTON

The only work on this crop has been the collection of *Nezara viridula* L. in Montserrat, and the rearing out of considerable numbers of *Trichopoda pilipes* F. for shipment to Australia against the same pest.

## BANANAS

The banana weevil, *Cosmopolites sordidus* Germ., causes considerable losses throughout the Caribbean area. *Plaesus iavanus* Er., a larval predator, was introduced from Fiji into Jamaica and was said to have reduced damage considerably. In 1942, 42 individuals were released in Trinidad and the species became well established. Since 1946 introductions of this species as well as those of a second species of histerid with similar habits and native to Trinidad, *Leionata quadridentata* F., have been made on an adequate scale in Grenada, Barbados, St. Vincent, St. Lucia, Dominica and the French Antilles. Whether they have become established is uncertain, but it has become increasingly clear that they would be of value only in poorly kept banana plantations, which nevertheless constitute a considerable part of the total cultivation. Where a high standard of cultivation is practised, modern persistent soil insecticides can keep plants absolutely free from weevil attack. It does seem that this is an example of the possibility of the complementary action of both biological and chemical control.

## ARROWROOT

*Calpodes ethlius* Cram., the arrowroot leaf-roller, is a serious pest of arrowroot, a crop of major importance in St. Vincent. In 1950 investigations of the parasites both in St. Vincent and in Trinidad were made with a view to biological control, with the result that several species of parasites were liberated in St. Vincent, the egg parasite *Ooencyrtus* sp. and the larval parasite *Apanteles calidicida* Wlkn., but apparently without establishment. This may be due to the very sporadic nature of the infestations of the pest. In Trinidad the butterfly breeds continuously on garden cannas and the population is kept at a low level by natural enemies. It is possible that if garden cannas (as opposed to *Canna edulis* which is not as acceptable to *Calpodes*) were planted around the arrowroot fields as a trap crop, parasites might be able to continue breeding and biological control become effective.

Several vegetable pests have been investigated: The white butterfly, *Pieris monuste* L., is seasonably a serious pest of cabbages in Barbados, St. Lucia, etc. Both *Pteromalus puparum* L. and *Apanteles glomeratus* L. were liberated. The former bred readily in the laboratory, the latter did not; it did, however, become quickly established in the field, whereas not a single recovery of *Pteromalus* was made. In the field the effectiveness of *Apanteles* in controlling *Pieris* appears to have been reduced by a hyper-parasite, *Elasmus* sp. Two other pests of cabbage have been investigated. No important parasites of *Hellula phidilealis* F. were found, and attempts at establishment of *Angitia*

*cerophaga* Grav. and *Diadromis collaris* Grav. in Antigua on *Plutella maculipennis* Curt. were unsuccessful.

A number of other biological control investigations have been carried out in Trinidad for areas outside the Caribbean, such as that on the weed *Cordia macrostachya* (Jacq.) R. & S. for Mauritius, the corn leaf worm, *Laphygma frugiperda* A. & S. and the pigeon pea podborer, *Ancylostomia stercorea* Zell., the lymexylonid *Atractocerus brasiliense* L. & S., for the Seychelles, the weeds *Stachytarpheta* spp. for Fiji, and the scale *Pseudaulacaspis pentagona* Targ. for Bermuda.

This brief list gives an idea of the scope for biological control work in the Caribbean area and it is certain that more intensive studies are likely to prove worthwhile.



# Biological Control in Some Commonwealth Countries

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In 1950 the delegates attending the Commonwealth Agricultural Bureaux Review Conference in London recommended that the Institute of Biological Control organize a commonwealth wide survey of the results obtained and the conclusions drawn from the biological work so far undertaken and that if possible the United States and possibly other countries be invited to collaborate. The object of this survey was, through a critical review of the work undertaken and an analysis of the reasons for success or failure, to determine how the empirical element in future projects might be reduced. Eventually a circular letter was sent out from our Ottawa office to thirty-one different points in the commonwealth asking for the information requested by the C.A.B. Conference. The persons and countries selected included all those from whom material of interest seemed likely to be available.

From ten of the persons approached no reply was received. Seven more stated that they had nothing to report. Four replied that material was being gathered as rapidly as possible and would be made available in due course. The federal entomologists of Australia replied in this sense as did the chiefs of the Divisions of Entomology and Forest Biology in Canada. The Canadian contribution to a survey of this kind is of course of absolutely major importance since in so far as the Commonwealth is concerned, it is in Canada that the most extensive operations and the most careful investigations connected with them have been carried out. Information on the work in the United States is of course also of the greatest importance but here the gap has been filled to some extent by a recent publication prepared by Mr. C. P. Clausen. From the survey he has made several considerations of general value emerge.

Although the survey even for commonwealth countries has remained quite incomplete I have thought it might be useful to the members of the section to have a brief summary of the results reported from the countries who have given positive answers to our letters of enquiry:

Since we have a very full programme it is necessary to be brief. I shall therefore confine myself mainly to the projects in which some measure of success is known to have been obtained.

In New Zealand a number of attempts have been made to control *weeds* by means of phytophagous insects. Against ragwort large introductions, extending over several years, of the leaf feeding caterpillar *Tyria jacobaeae* and the seed-fly *Pegohylemyia jacobaeae* were made. *Tyria* established itself in one or two localities and persisted in one district for several years before virtually disappearing. A heavy attack by native parasites and by a New Zealand cuckoo and other birds apparently prevented this insect from becoming effective. The seed-fly was established but nothing definite is known at the present time as to the degree of control it has produced. Against St. John's wort the chrysomelid beetle, *Chrysolina hyperici*, has given outstanding results. Extensive areas of the weed have been cleared and replaced by pasture. A seed-weevil attacking gorse was introduced some twenty-five years ago from England and is now widely established throughout New Zealand. It has produced a large reduction in seed but not sufficient to prevent the spread of gorse, one important point being, that the seed pods of the second flowering are not usually attacked by the weevil, which is normally single brooded. A curious case which deserves mention is that of the spectacular control of Manuka of which the scientific name is *Leptospermum scoparium*, by the coccid *Eriococcus manukae*. No one knows whether this coccid is a native species which has suddenly become abundant or an introduced form. However it is known that a scale on a weed of the genus *Metrosideros* which was certainly uncommon in the first decade of this century is now so abundant that extensive areas of the plant have foliage encrusted by it and rendered grey in colour.

Turning to the biological control of insects there is reasonable certainty that a number of experiments in New Zealand have given good results.

The Australian *Eriococcus coriaceus* destroyed many plantations of eucalyptus early in the century but the ladybird, *Rhizobius ventralis*, when introduced against this insect gave spectacular results and since that time there have been no outbreaks of any importance. The eucalyptus weevil, *Gonipterus scutellatus*, has also been satisfactorily controlled by the myarid egg parasite, *Anaphoidea nitens*, introduced from Australia. The golden oak scale (*Asterolecanium variolosum*) played havoc with English oaks at one time, but the introduction from North America of *Habrolepis dalmani* reduced the numbers of the pests to such an extent that when an effort was made to secure the parasite for Chile it was found very difficult to find any specimens of the scale. Among field crop insects, the cabbage butterfly, *Pieris rapae*, which was once extremely abundant and destructive on crops in New Zealand was controlled very rapidly by the introduction of the pupal parasite, *Pteromalus puparum*, and the larval parasite, *Apanteles glomeratus*. An interesting fact about this case, if I remember correctly, is that although large numbers of *Apanteles glomeratus* collected from *Pieris brassicae* were sent to New Zealand the species did not become permanently established, and satisfactory results were obtained only when what supposed to be the same parasite was introduced from North America where it attacks *Pieris rapae*. I believe that *Apanteles glomeratus* does not usually attack *Pieris rapae* in Europe except when it is scattered through a population of *Pieris brassicae*. There has never been any suggestion that there are two distinct races of the *Apanteles*, one confined to *brassicae* and the other to *rapae* but there is certainly something here that merits further investigation. According to Dr. David Miller who has supplied me with this information the diamond back moth, *Plutella maculipennis*, is now satisfactorily controlled by the ichneumonids, *Angitia cerophaga* and *Diadromus collaris*. However there was already in New Zealand an *Angitia* very closely allied to *Angitia cerophaga*, so closely allied indeed that one wonders whether it is possible to distinguish the imported from the native material present in the field. Nevertheless according to the entomologists in New Zealand the importation of the parasite *Angitia* from England had a very marked effect on the general position.

In South Africa a considerable number of experiments in biological control with introduced material has been made.

As in other countries biological control of the cottony cushion scale by *Novius cardinalis* and of the woolly aphis of the apple by *Aphelinus* has been obtained in South Africa. Good control of the mealy bug, *Pseudococcus citri*, on citrus has been obtained in the Cap Province and the Transvaal by the artificial propagation of *Cryptolaemus* though certain ants, when present, interfere very seriously with this.

A very important and spectacular success in South Africa is of course the control of the eucalyptus weevil, *Gonipterus scutellatus*, by the mymarid *Anaphoidea nitens*. I have already referred to this case in connection with New Zealand. In South Africa the damage done by the weevil was apparently much more important and the project is of particular interest inasmuch as it is a case where success was achieved over a large sub-continental area with a use of a single parasite and this parasite is one which would appear to be very delicate and susceptible to environmental changes and yet was successful over a great variety of ecological conditions raising from coastal conditions to 6,000 feet above sea level, winter rainfall to summer rainfall, subtropical to temperate, mild wet winters to very cold winters of six to nine months drought. It had to adapt itself to a considerably changed life-history of its host as compared to the conditions under which both occur in South Australia. Another point worth noting here is that where the parasite gained complete control over its host in areas of good rainfall and good tree growth it took over twenty-five years to gain ascendancy in the areas less suitable for tree growth, soil temperature and rainfall. Nevertheless the change in favour of the parasite's ascendancy has in these areas been very gradual but positive. Results have been evident not only in the gradual improvement of main susceptible eucalyptus, to wit — *Eucalyptus viminalis* — but also in a gradual reduction of the number of species showing signs of attack. At the outset twenty-two species were so severely attacked that they could not be recommended for planting locally. Nine were severely attacked under certain conditions and thirty-four relatively lightly. At present only three species show appreciable attack under adverse conditions the rest having

joined the ranks of the virtually immune species under conditions prevailing in the South African Union.

I now turn to the Colonial areas from which we have received some reports.

Dr. H. C. James supplied information for Jamaica. Some abortive but rather curious experiments in biological control were made in Jamaica. They would certainly interest you if we had time to discuss them but I can only mention one and that is the introduction in 1762 from Cuba of the ant, *Formica rufa*, which has since been known as the Tom Raffle ant, because Thomas Raffle brought it in. The object of this introduction was the reduction of the number of rats in canefields. It is said that they were useful for many years but now are apparently themselves a fairly serious pest.

One of the first outstanding successes in modern times was the introduction by the late Dr. J. G. Myers, who was then on our staff, of the eulophid parasite, *Eretmocerus serius*, attacking the citrus aleurodid called the citrus black fly. Consignments of this were brought into Jamaica in 1932 and the parasite spread rapidly. By the end of 1934 it became possible for the Department of Agriculture to report that the citrus black fly was considered to be completely under control over the whole island.

It is said also that the black histerid beetle, *Plaesius javanus* (Er.), which is predatory on the banana weevil borer, *Cosmopolites sordidus*, and was introduced in 1918-1919 from Java, has proved to be a very useful auxiliary in the fight against the pest.

Finally, a group of coccinellids predacious on the coconut scale, *Aspidiotus destructor*, and introduced from Trinidad has considerably reduced the incidence of the scale in the islands of Grand Cayman and Cayman Brac.

In Cyprus, biological control work has been limited to the introduction and distribution of the chalcid, *Aphelinus mali*, against the woolly aphis of the apple and the coccinellid, *Novius cardinalis*, against the cottony cushion scale. These parasites were brought in in 1937 and 1938 and since they became established and distributed through the island no serious outbreaks of the pests have occurred.

In the island of Fiji several outstanding successes have been obtained in the field of biological control. The most important of these were the control of *Levuana iridescens*, the second the control of *Aspidiotus destructor* and the third the control of the leaf mining beetle, *Promecotheca reichei*. All these were pests of coconuts. An ichneumonid parasite of a rice leafroller, introduced in 1935 is said from 1948 onwards to have given excellent control of this pest. A species of *Apanteles* introduced against the rice armyworm in 1950 is believed to have had successful results since the parasite became established in great numbers and since that time there have been no serious outbreaks of the insect.

Malaya has provided parasites and predators which have been successfully utilized in other countries against the pest they attack and this indicates that native Malayan parasites must be of considerable importance but there have been few importations of material into Malaya and these have not so far given satisfactory results.

In the Colony of Kenya a remarkable and outstanding success has been obtained in the biological control of the coffee mealybug, *Planococcus kenyae*. Before the establishment of effective parasites, says Dr. LePelley, the mealybug was an outstanding major pest of coffee on many African food crops in an important part of the Central Province of Kenya. It was apparently introduced just before 1923 when the first heavy attacks occurred and from then until 1939 it was estimated that the loss due to this pest was between £1,000,000 and £1,500,000 and at times it appeared that this plantation industry might fail because of the mealy bug. Parasites and predators were introduced over a considerable period, in fact the work began in 1929 and continued until 1953. Parasites were brought in from many parts of the world but no practical results were obtained until the establishment of *Anagyrus* nr. *kivuensis* (Comp.) which was introduced from Uganda in 1938. According to Dr. LePelley, following the first liberations of this species a remarkable clean-up of mealy bug occurred. The parasite reduced the bug rapidly and effectively from the position of an outstanding major pest to that of a minor pest causing very little general loss. This position has been maintained to a large extent though from time to time and from place to place there are attacks

of severity on coffee due apparently to the injurious action of indigenous hyperparasites. The successful biological control of the coffee mealy bug has contributed greatly not only to the prosperity to the coffee industry but to the economy of the country as a whole. The control exerted by the parasites in native grown coffee has been even greater than in large coffee plantations and in these areas, says Dr. LePelley, the mealy bug has become a rare insect. If it had not been successfully controlled the native coffee industry which is now rapidly expanding and developing could never have got underway.

Other successful experiments in Kenya are the control of the woolly apple aphid, of the eucalyptus weevil and to some extent of the scale, *Orthezia*.

Considering the cases reported, both successful and unsuccessful, the main conclusion that emerges is that we do not know nearly enough about the material we are attempting to use in biological control work. To begin with, we need much more accurate and detailed systematic work, even on the adult material in our collections. A detailed study of larval stages will often be useful not only to interpret the results of dissections of field-collected material but also because it may suggest studies leading to the separation of forms now lumped under one name and help in the definition of taxonomic categories. More detailed laboratory studies on the ecological requirements of parasites and predators are needed because we can now list a large number of cases in which the natural enemies cannot exist or cannot flourish although their hosts are quite common. It is clear that the methods of modern genetics must be brought to bear on these problems, keeping always in mind the objective of analysing the characteristics of populations in relation to environmental conditions. Finally, it is necessary to determine what part parasites really play as economic agents. In the Canadian Green River Project an intensive effort in this sense is being made but much more remains to be done. We cannot expect that these investigations will in all or even in many cases, enable us to achieve practical results more easily. But at least they should enable us to understand our failures and the importance of this in biological control work, can hardly be exaggerated.



# Biological Control of Insect and Plant Pests in Canada<sup>1</sup>

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## ABSTRACT

Some of the earliest records of entomological work in Canada include references to the use of beneficial insects, and with the co-operation of entomologists in the United States, the Commonwealth Institute of Biological Control and many foreign countries, biological agents have been used to advantage in the control of many major pests.

In the 45-year period, 1910-55, a total of nearly a billion individuals of some 220 species of insect parasites and predators have been released against 68 species of pest insects, and four species of phytophagous insects have been released to assist in the control of St. John's Wort (*Hypericum perforatum* L.). More than 50 beneficial species have become established and some of these are extremely valuable control agents. The possible use of disease organisms is being thoroughly investigated and its value has been demonstrated in control of one forest pest by a virus.

Historical aspects of biological control work in Canada have been given in some detail in the special Congress issue (July 1956) of *The Canadian Entomologist*, and I will, therefore, confine my remarks largely to reviewing some of the projects undertaken.

It is natural that the biological method of pest control has had a strong appeal to Canadians and has been used extensively for more than half a century (roughly coinciding with the period covered by international congresses). A vast country with a comparatively small and scattered population, extensive and, at times, ruthless exploitation of natural resources has provided optimum conditions for rapid increase and spread of pests, and mass immigrations from European countries in settlement of the country bringing plants and insects often without natural enemies have contributed to the creation and development of serious pest control problems. Control by chemicals has been limited economically and until recent years could be applied only on concentrated, cultivated crops of high value.

The fact that many of the insect pests came from Europe led to early efforts to introduce natural enemies and thus to ensure re-establishment of the balance of nature in this new country. Such work in Canada has largely followed or paralleled developments in the United States and early successes such as attended introduction of the vedalia beetle into California encouraged further attempts. The two countries have worked as one in obtaining material and information as well as in their utilization. Entomologists throughout the world have been very co-operative and the Commonwealth Institute of Biological Control, formerly Farnham House, has given important help in Europe.

Introduced sawflies of many species have been among the most serious forest pests. In the late years of the 19th century the larch forests of Eastern Canada and the United States were almost completely destroyed by the devastating feeding of the large larch sawfly, *Pristiphora erichsonii* (Htg.), thought to have been introduced from Europe. The infestation persisted on the younger growth, spreading across the continent and was found in British Columbia in 1933. An important larval parasite, *Mesoleius tenthredinis* Morley, introduced from England in 1910-13 and colonized and re-colonized across the continent, proved a major factor in preventing destruction of the new larch forests in the East and the extensive stands of western larch in British Columbia. In most areas where the parasite was colonized the build-up was rapid and outbreaks were reduced in three to five years. An exception is an area across north-western Ontario, and the northern part of the Prairie Provinces where *M. tenthredinis* persists at a low level with little controlling effect because of encystment of a large percentage of the eggs deposited in host larvae. Is this a different race or species of sawfly, or are environmental conditions responsible?

<sup>1</sup>Contribution No. 3557, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.



The spruce sawfly, *Gilpinia hercyniae* Htg., another import from Europe, discovered in eastern Quebec in 1930 bid fair to repeat the story of devastation, this time on the more valuable spruce forests. Introduction of parasites carried out between 1931 and 1939 included also natural enemies of a number of similar or closely-related species of sawflies attacking spruce and pine. Thirty-one species were released and some ten or twelve species became established in the areas of heavy infestation present between 1933 and 1940. A cocoon parasite, *Dahlbominus fuscipennis* (Zett.), of which more than 850 million were released, assisted greatly in the rapid reduction of accumulated stocks of diapause larvae in cocoons. (In some areas these were so abundant from several years' accumulation that 20- to 30 thousand could be collected from the moss and debris per man day). Two larval parasites, *Drino bohémica* Mesn. and *Exenterus vellicatus* Cush., were specific enemies of *G. hercyniae* and continue to destroy important percentages of larvae thus preventing development of local outbreaks and reducing the rate of westward spread. It is believed also that the virus disease responsible for the rapid decline of the outbreak generally was fortuitously introduced and distributed with the parasites. Several species have proven of great value in reducing infestations of pine sawflies, including the introduced *Neodiprion sertifer* Geoff. and *Gilpinia frutetorum* Fabr. and the native *N. lecontei* Fitch.

Whether European parasites of the brown-tail moth, *Nygmia phaeorrhoea* (Don.), colonized between 1913 and 1917, were important agents in eradicating this pest may be open to question but, in any case, the larval parasite, *Compsilura concinnata* L., introduced at that time, has aided in the control of many native pest species and has had much to do with keeping the satin moth, *Stilpnotia salicis* (L.), from becoming a more serious pest.

Just prior to the outbreak of World War II, four species of parasites of the larch casebearer, *Coleophora laricella* Hbn., were brought from England and released in an infested area north of Belleville. By 1945, combined parasitism reached almost 100% and in 1946 the value of this was clearly demonstrated, the foliage of the trees being completely green at the centre of liberation and the degree of defoliation increasing gradually to complete defoliation at a radius of ten miles. Material collected in this area was used in establishing colonies of the parasites at other points in the eastern provinces.

Among projects at present in progress might be mentioned colonization of parasites of the pine shoot moth, *Rhyacionia buoliana* (Schiff.), in Ontario, the winter moth, *Opherophthera brumata* (L.), in Nova Scotia, and an exhaustive program of introduction of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.), which will be discussed fully at our session on August 25th.

Control of a number of orchard pests has been aided greatly by introduction and transfer of parasites and predators. Among the most spectacular was the effect of colonization of a larval parasite, *Macrocentrus ancyliivorus* Rohw., in reducing the outbreak of oriental fruit moth, *Grapholitha molesta* Busck., which threatened the peach industry in Ontario in the 1920's. This parasite, introduced from New Jersey in 1929-30, has maintained its place as an important control factor through rapid development of strains resistant to DDT and other chemicals used in general orchard practise. The oyster shell scale, *Lepidosaphes ulmi* (L.), was reduced to a minor pest in British Columbia by the predacious mite, *HemisarcOPTES malus* (Schimer), transferred from New Brunswick in 1917, the apple woolly aphid, *Eriosoma lanigerum* (Hausm.), by the transfer of *Aphelinus mali* (Hold.) from Ontario in 1929-30, and the apple mealy bug, *Phenacoccus aceris* (Sign.), in British Columbia by transfer of *Allotropa utilis* Mues., from Nova Scotia. Introduced parasites have also given valuable help in control of the holly leaf miner, *Phytomyza illicis* (Curt.), the hazel nut scale, *Lecanium coryli* (L.) and Comstock's mealy bug, *Pseudococcus comstocki* (Kuw.).

Among field crop and garden pests, the pea moth, *Laspeyresia nigricana* (Steph.), was reduced to minor importance in British Columbia by two parasites, *Ascogaster quadridentatus* Wesm. and *Glypta haesitator* Grav., introduced from England between 1937 and 1939. They have later been recolonized in the Eastern provinces. The European wheat-stem sawfly, *Cephus pygmaeus* L., has been controlled in Ontario by two species of parasites, *Collyria calcitrator* (Grav.) and *Pleurotropis benefica* Gahan, introduced from England. The same species of parasites have not

proven successful against the Western wheat-stem sawfly, *Cephus cinctus* Norton, although quite satisfactory initial establishment followed large releases in several areas.

For more than 25 years the parasite, *Encarsia formosa* Gahan, was propagated at the Belleville laboratory and stocks supplied on request to growers of greenhouse crops of tomatoes, cucumbers and other crops susceptible to attack by the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.). This parasite gives very effective and economical control of the pest when the recommended temperature range is maintained.

The effect of diseases on insect abundance has been under investigation for many years and numerous attempts have been made to develop their use in control of pests. The first success in this field in Canada was the technique developed for use of the fungous disease, *Entomophthora sphaerosperma* Fres., by which the apple sucker, *Psylla mali* (Schmidt), was practically eliminated from certain orchards in Nova Scotia in 1922-23. Unsuccessful efforts were made to utilize disease organisms in control of the brown-tail moth, the larch sawfly, the European corn borer and many others. However, the remarkable results following development of the virus disease in the spruce sawfly larvae and later success in reducing infestations of the pine sawfly, *Neodiprion sertifer* (Geoff.), by a virus organism introduced from Europe have led to greatly increased interest in the study of microorganisms occurring in insects in the hope that techniques for their utilization can be developed. Work in this field is in progress at Belleville and Sault Ste. Marie, Ontario.

The biological control of weeds was undertaken for the first time in Canada in 1951 with introduction of two European chrysomelid beetles, *Chrysolina hyperici* (Forst.) and *Chrysolina gemellata* Rossi, for control of the common St. John's Wort, *Hypericum perforatum* L., in British Columbia. Stock of the beetles was obtained by collection in California, Oregon, and Idaho. Both species are well established and the results are being followed with interest. Two additional species, *Agrilis hyperici* (Creutzer) and *Zeuxidiplosis giardi* Kieff., were released in 1955.

The examples given show the broad field of coverage and although the forest has perhaps presented the greatest opportunities and economic returns from utilization of this method of pest control, it has been of equal value, relatively speaking, in the case of many other serious pests. In the period since 1910, some 220 species of insect parasites and predators have been released against 68 species of insect pests and four species of phytophagous insects have been released to assist in the control of an important weed. Disease organisms have been used in a more limited way with successful results in two cases. Through the years, a great deal of attention has been given to obtaining basic information on the factors responsible for regulating insect populations and problems associated with the effective use of biotic agents in control of pest species. The aim at all times has been to take care of emergency control requirements in the best manner possible but with a long range view to having biological control fit in with land and crop management plans that will reduce pest losses to a minimum.



# Parasites of the European Corn Borer in the United States

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## ABSTRACT

Early in the known occurrence of the European corn borer in the United States, an extensive program for exploration of parasites of the borer, and their introduction into the United States was initiated in Europe and the Orient. Since that time 24 species have been collected and forwarded to the U.S., 22 of which were available for extensive release over the borer infested area. Of these, 6 species have become established in the United States, and 5 species have become sufficiently abundant in one or more areas to be of aid in the natural control of the borer. Each of these species, however, expresses its principal beneficial effect on subsequent populations rather than on the immediate population parasitized. Accordingly, the parasites must be evaluated in terms of their ability to depress succeeding borer populations in competition with other factors having similar effects, such as destruction of borers by normal farm practices, insecticide applications, weather factors and relation of growth stage of the host plant to borer infestation and survival. Observations to date have established that the parasites do not have an efficiency adequate to provide complete control of the borer and an appraisal of their effectiveness as a partial control factor on a quantitative basis is extremely difficult. The problem may be defined as the relation of the carrying capacity of the environment, or the borer population that would occur in the absence of parasites, to the biotic potential of the pest. The effect of parasites as an additional factor in the environment is reflected as they reduce the host biotic potential below the carrying capacity of the environment. As it has not been possible to isolate the impact of parasitism on the biotic potential of the borer from the many other factors exerting a similar effect, appraisal of their effectiveness as an aid in natural control is made on the basis of percentage of parasitism attained, associated with borer population trends, rather than effect on borer biotic potential.

One of the larger programs that has been undertaken in the United States for investigating and utilizing parasites of an introduced pest in its control has been directed against the European corn borer *Pyrausta nubilalis* (Hbn.). This pest was first recorded in this country infesting sweet corn in the vicinity of Boston, Mass., in 1917. It presumably originated in shipments of broomcorn from Hungary or Italy during the period 1909-14. The seriousness of the pest was recognized immediately, and in the fall of 1919 plans were initiated for exploration of the parasite fauna of the corn borer in Europe, and subsequent importation of various species into the United States. The European phases of the program were developed under the able direction of W. R. Thompson, assisted by Harry Parker early in the program, and who later succeeded him. The work in Europe was supplemented by similar observations and shipments of parasite material from the Orient from 1927 to 1936, first under the direction of W. B. Cartwright and later C. A. Clark.

This program has resulted in the importation of 24 species of parasites, 22 of which have been available in sufficient numbers from direct importation, laboratory increase, or domestic collections for extensive test releases over borer-infested areas in the United States. Many of these species were also available for forwarding to Canada for inclusion in their biological-control program through the cooperative endeavors of A. B. Baird, head of the Biological Control Unit of the Entomology Division of Science Service, Canada Department of Agriculture, and D. W. Jones, formerly in charge of the domestic European corn borer parasite program for the United States Department of Agriculture's Bureau of Entomology and Plant Quarantine. The domestic corn borer biological control investigations are now being directed by G. T. York, at the Ankeny, Iowa, laboratory of the U.S.D.A.'s Entomology Research Branch.

Of these 22 species, 6 have become established in the United States, and 5 — *Lydella grisescens* (R. D.), *Macrocentrus gifuensis* (Ashm.), *Chelonus annulipes*

(Wesm.), *Horogenes punctorius* (Roman), and *Sympiesis viridula* (Thomson) — have become sufficiently abundant in one or more areas to aid in the natural control of the borer. The sixth species, *Phaeogenes nigridens* (Wesm.), which is the only imported pupal parasite of the borer, became well established in eastern Massachusetts early in the release program, but apparently has not built up in sufficient numbers to have much effect on population levels.

Each of these species expresses its principal beneficial effect on subsequent host populations rather than on the immediate population parasitized as they have shown little or no ability to limit feeding and activity of the borer before causing its death at time of maturity. Consequently, the beneficial effects of the parasites must be evaluated in terms of their ability to depress succeeding borer populations in relation to other factors having the same effect, such as normal farm practices, insecticide applications, weather, relation of the growth stage of the host plant to borer infestation and survival, and the natural intrinsic weakness of the borer. The last two factors are of particular importance in evaluating borer-population fluctuations. Normally there is a 90-95 percent reduction between the eggs and 4-day old larvae, associated with their efforts to survive and become established on their host plants. During the early feeding period they express their combative characteristics while attempting to secure favorable establishment locales. Furthermore, larval establishment varies as much as 90 percent from survival during the early stage of plant growth to survivals when infestation takes place during the early tassel stage, which is apparently the optimum growth stage for borer establishment and survival.

Thus far, in the areas in which one or more of the parasites have become prominent in the general biological complex, they do not provide complete control of the borer. In general, the parasitism has ranged from 25 to 50 percent, and in some restricted localities *Lydella* has parasitized as high as 90 percent. Accordingly, we are dealing with a partial control factor only, and a quantitative appraisal of a parasite's effectiveness in relation to the many other factors involved is extremely difficult.

The problem may be defined as the relation of the carrying capacity of the environment, or the borer population that would occur in the absence of parasites, to the biotic potential of the pest insect. The effect of parasites as an additional factor in the environment is reflected as they reduce the host biotic potential below the carrying capacity of the environment. We can therefore expect no benefits from parasitism until it attains such a magnitude as will cause this amount of host reduction. In pursuing this philosophy when appraising field results, we must assume that in any one year at any one location the carrying capacity of the environment is a finite quantity, but that it may, and probably does, vary from place to place and year to year. However, this assumption does not detract from the basic philosophy. In fact, it further emphasizes the complexities involved in developing an adequate statistical treatment of data as an appraisal of the parasites' effectiveness.

As it has not been possible thus far to isolate parasitism from the many other factors affecting the biotic potential of the borer, current appraisal of its effectiveness is made on the basis of percentage of parasitism attained rather than on borer biotic potential.

A brief summary, by States, will be presented here of the current status of those imported parasites of the borer that have become established in the United States and for which we have recent field data.<sup>1</sup> The data are for the years 1952-54, as assembled in the accompanying table (Table I). In general they were obtained by the sampling methods and subsequent handling of the field-collected larvae for laboratory rearing as detailed by Baker *et al.*<sup>2</sup>

Status collections are made for several purposes. Those made soon after the original introduction and release of a species furnish information on whether or not

<sup>1</sup>Agricultural Experiment Stations and/or Departments of Agriculture in the following States have cooperated closely in this program, particularly in making parasite releases and subsequent collections of larvae to determine their establishment, maintenance, and effectiveness, Alabama, Connecticut, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Dakota, Ohio, Pennsylvania, Rhode Island, South Dakota, Tennessee, Virginia, West Virginia, and Wisconsin.

<sup>2</sup>Baker, W. A., W. G. Bradley, and C. A. Clark, 1949. Biological control of the European corn borer in the United States. U.S. Dept. Agr. Tech. Bul. 983: 185 pp.



TABLE I — Average Percent Parasitism from Selected State Areas 1952-1954.

STATE	PARASITE					TOTAL
	Lydella grisescens	Macrocentrus gifuensis	Chelonus annulipes	Horogenes punctorius	Sympiesis viridula	
Maine	O*	T**	—***	—	—	T
New Hampshire	—	—	—	O — 4	—	2
Massachusetts	T	24 — 27	T — 1	T	O	26
Rhode Island	1	26	O	O	O	27
Connecticut	T	18 — 28	T — 2	T	O	24
New York	T — 3	4 — 6	O	T — 4	T	9
Pennsylvania	10 — 27	3 — 4	O	O	O	22
New Jersey	3 — 16	2 — 6	—	T — 1	O	13
Maryland	8 — 18	T — 5	O	T	O	12
Virginia	T — 1	O	O	O	—	T
Ohio	17 — 34	O	O	T — 3	T — 1	27
Michigan	10 — 20	O	O	T — 1	O	15
Wisconsin	9 — 18	O	O	O	T	7
Illinois	7 — 33	O	O	T	T	21
Iowa	9 — 15	T	O	T	T	13
Minnesota	10 — 22	O	O	1 — 2	T — 2	18
North Dakota	O	O	O	O	T	T
Nebraska	3 — 44	O	O	O — 1	O	24
Kansas	T — O	O	—	—	—	T
Missouri	19 — 35	O	—	—	—	27
Tennessee	T	O	O	—	—	T

\*O = releases and recovery collections.  
 \*\*T = less than 1 percent parasitism.  
 \*\*\*— = either no releases or releases but no recovery collection.

it becomes established. If establishment is obtained, collections during the following years show its rate of spread and, in case a species becomes established over a wide area, the fluctuations in population density. Where several species are established in the same area, the relative importance and the population fluctuations of the different species are obtained.

Several areas in the first category — that is, the establishment of a species — are still under consideration. These areas include those involving redistribution of a species already established in the United States and those receiving releases of new introductions. The importation program is now under the direction of T. R. Gardner, of the Entomology Research Branch. All the species that are established are currently being redistributed in the more southern areas of corn borer dispersion, following its southern extension and recent buildup to economic numbers in certain sections, particularly in Alabama, Oklahoma, and Tennessee. In addition, *Campoplex alkæ* (Ell. and Sacht.) was liberated in Minnesota in 1953. This is not strictly a new species, since it was introduced earlier but failed to become established. It has not yet been recovered in Minnesota. In 1954 four species from India, originally introduced as parasites of the pink bollworm, were released in New Jersey, and two of these species were released in two localities in Iowa. The 1954 collections failed to show establishment of any of these parasites.

Most states showed from slight to marked declines in percent parasitism from 1952 to 1953. Illinois showed the greatest reduction, from 33 percent to 10 percent. It was followed by Pennsylvania with a reduction from 30 percent to 14 percent. Only three states — Minnesota, Wisconsin, and Ohio — showed increases.

Results between 1953 and 1954 were more variable. Some states continued to show a decline; Minnesota was the only state that showed a continued increase.

CONNECTICUT.—The average parasitism for the years 1952, 1953, and 1954 were 29, 22, and 19 percent, respectively. Surveys of the eastern two-thirds of the state were made in 1952 and 1953. That portion of the state was divided into 10-mile squares and samples were taken from each square. In 1954 the western portion of the state was similarly divided, and the entire state "checkerboard" sampled. *Macrocentrus* was the predominant parasite, accounting for most of the parasitism in all 3 years. *Chelonus* was well established in a few areas, parasitizing 45 percent of the borers in Hartford County in 1953. Both *Horogenes* and *Lydella* were at a very low level in all three years.

ILLINOIS.—State averages for 1952, 1953, and 1954 were 33, 10, and 7 percent, respectively. Practically all the parasitism was by *Lydella*. One specimen of *Horogenes* was taken from northwestern Illinois in 1953 and another in 1954, showing that the species still persisted. The cause of the marked drop from 1952 to 1953 is not known, but it is suspected that hot, dry weather had a deleterious effect on *Lydella*, both in decreasing the longevity of adults and making it more difficult for the young larvae to find a host.

IOWA.—State averages for the years 1952, 1953, and 1954 were 10, 9, and 15 percent, respectively. *Lydella* was responsible for practically all the parasitism of overwintering borers. One specimen of *Macrocentrus* was taken from Clayton County in 1952 and again in 1954, and one from Howard County in 1953. Both counties are in northeastern Iowa. Collections on a county basis were so small that there may be a higher population of *Macrocentrus* than these figures indicate. One specimen of *Horogenes* was taken in Jackson County and one in Jones County in 1953. Although the average parasitism in Iowa has remained fairly constant during the three years, there has been a noticeable shift in the areas of maximum intensity. In 1952 the highest parasitism, 30 percent, was in the eastern and southeastern parts of the state. The 1953 collections showed the highest parasitism of 31 percent in the northeastern corner of the state, with 25 percent to the south and 15 percent to the west. In 1954 the highest parasitism was still in the northeast at 36 percent, but in the center of the state it was approximately 25 percent. Hence, although the northeastern corner remained high, there was a general shift to the central portion of the state.

KANSAS.—Only one parasite, *Lydella*, was recovered in 1952, and the two succeeding years failed to show any parasites. If *Lydella* has not been eliminated from Kansas, it is at least at an extremely low density.

MAINE.—Collections were received only in 1952, and only one borer was infested, and that with *Macrocentrus*.

MARYLAND.—State averages for 1952, 1953, and 1954 were 23, 9, and 13 percent, respectively. *Lydella* was the most abundant species. *Macrocentrus* was recovered each year but in diminishing percentages from 1952 to 1954. *Horogenes* was found only in 1954.

MASSACHUSETTS.—Rather extensive collections were made in 1952 and 1953, by S. W. Carter, of the Entomology Research Branch. They were discontinued in 1954 because of limited personnel and funds. Collections were made on the 10-mile-square grid basis and were contiguous with Connecticut collections. Parasitism was 28 percent in 1952 and 26 percent in 1953. As in Connecticut, *Macrocentrus* was the predominant species. Less than 1 percent was attributable to *Lydella* and *Horogenes*. Although *Chelonus* was taken in several collections in the southeastern part of the state, the average for the state was only slightly more than 1 percent. The highest parasitism by this species was 41 percent from a collection taken near New Bedford.

MICHIGAN.—Collections were limited to the study area in Monroe County in the southeastern corner of the state. Parasitism was 22 percent in 1952 and 10 percent in 1953. *Lydella* was the predominant parasite, but a few specimens of *Horogenes* and *Sympiesis* were taken.

MINNESOTA.—The program of releasing parasites in counties where the borer had spread but parasites were not known to be present was continued. The average parasitism in 1952 was 13 percent, in 1953 18 percent, and in 1954 24 percent.

MISSOURI.—Borers were collected only in one area in the southeastern corner of the state during the 3-year period. In 1952 no parasites were recovered. In 1953 the field collections showed 35 percent parasitism by *Lydella*. In 1954 two collections from Scott County and one from Mississippi County showed approximately 20 percent parasitism and all by *Lydella*.

NEBRASKA.—Collections were made only in Lancaster County, where parasites were liberated in 1950. Parasitism by *Lydella* reached 44 percent in 1952. In 1953 no parasites were recovered from comparable collections. The 1954 collections gave 3 percent parasitism, showing that *Lydella* had persisted even though it was not recovered in 1953. The other two parasites released in 1950, *Horogenes* and *Macrocentrus*, were not recovered during this 3-year period.

NEW HAMPSHIRE.—Collections were received only in 1952 and parasites were recovered.

NEW JERSEY.—Collections were extensive in 1952 and 1953, being made on the 10-mile-square basis as in New England. In 1954 they were reduced to one collection near the center of four previous collections, or one collection per 400 square miles. They were considered sufficient for comparisons with previous years in giving a general picture of the parasite situation in the state. Parasitism for the three years was 23, 12, and 6 percent. *Lydella* was the most abundant species, accounting for 16, 7, and 3 percent. *Macrocentrus* showed a similar decline, going from 6 to 3 to 1 percent. The population of *Horogenes* was low each year, being at about 1 percent. Causes of the decline are not known.

NEW YORK.—State totals are from two widely separated areas, one in the western portion and the other from Long Island. The percentages for the three years are 11, 10, and 5. *Macrocentrus* was the predominant species on Long Island, with a few *Horogenes*, but no *Lydella*. In the western area *Horogenes* was the most abundant, followed by *Lydella*, but no *Macrocentrus*. Since no collections were received from western New York in 1954, the state total is in reality the Long Island total and does not necessarily indicate a decrease in the *Horogenes* and *Lydella* population.

NORTH DAKOTA.—Only four collections were received in 1952, and they failed to show any parasites. No collections have been received since 1952.

OHIO.—Only in 1952 could collections be considered fairly representative of the state. The average parasitism for that year was 19 percent. *Lydella* accounted for nearly 17 percent, and the remainder was due to *Sympiesis* and *Horogenes*. No specimens of *Macrocentrus* were recovered in any year. In 1953 collections were made only in the study areas in Erie and Lucas Counties. Parasitism in Erie County was 53 percent, a sharp increase from the 20 percent of the previous year. In contrast, Lucas County showed 16 percent for the two years. Collections in 1954 were from the Erie County study area and an adjacent area in Huron County, 20 miles south of Lake Erie. The average parasitism in all collections was 26 percent. As in the other north-central states, *Lydella* was most abundant, accounting for 23 percent of the parasitism. *Horogenes* was next with 3 percent. Although this is a low percentage, *Horogenes* is probably more abundant in Ohio than any other state where records are available. The Erie County collection showed 38 percent parasitism by *Lydella*, and Huron County, 20 percent. Such a difference, would indicate a greater parasitism along the lake shore than inland. However, the collections at Wooster, about 50 miles south of Lake Erie, showed a parasitism of 29 percent. Such data indicate a wide variation in parasitism, and although it might be generally higher adjacent to the lake shore, rather extensive collections would be necessary to verify the point.

PENNSYLVANIA.—Collections were taken only in 1952 and 1953. In 1954 the borer population was so low it was considered impractical to conduct the parasite-status

survey. Parasitism in 1952 was 30 percent, but in 1953 it dropped to 14 percent. *Lydella* was the major parasite, and the entire drop was due to the reduction of this species. *Macrocentrus* was the only other exotic parasite recovered. It accounted for 3 percent parasitism in 1952, and 4 percent in 1953.

RHODE ISLAND.—Collections were made only in 1952. As in Massachusetts and Connecticut, *Macrocentrus* was the predominant species, accounting for 26 percent of the total 27 percent parasitism.

TENNESSEE.—Collections have failed to show any parasites since 1953, although a few *Lydella* specimens were taken from the northern part of the state in previous years. A few were released in 1953, and liberations of *Macrocentrus* and *Chelonus* were made in the Nashville area in 1954.

VIRGINIA.—Collections in 1952 and 1953 indicated a very low parasite population. *Lydella* was the only exotic species recovered, amounting to about 1 percent in both years.

WISCONSIN.—The average parasitism, as determined from all collections, was 9, 19, and 11 for the years 1952, 1953, and 1954, respectively. *Lydella* accounted for virtually all of the parasitism. The only other exotic parasite recovered was one specimen of *Sympiesis* taken in 1953. Collections from Wisconsin were taken on a district basis, with supplementary collections in 1952 and 1953. The state is divided into eight districts. Although the supplementary collections altered the changes in parasitism, the same general trend of the state averages was maintained. In other words, on the basis of just the district collections, the averages were 3, 15, and 11 for the three years. These figures show an increase from 1952 to 1953, and a slight drop from 1953 to 1954.

Although our field collections for 1955 throughout the borer-infested areas of the United States were not so extensive as in previous years, it is evident that the maximum concentrations of *Lydella* are in Ohio and Illinois, approximating 25 percent in each of these states. In general, *Lydella* is the most effective of the imported parasites in the north-central states, and *Macrocentrus* in the eastern states. The other species, while persisting in the biological complex at scattered localities throughout the infested area, have not become sufficiently numerous to affect borer populations to any appreciable extent. We will be extremely interested in following the parasitism trends of the various species as they are released and have had an opportunity to become established and stabilized in the more recently infested areas of the United States as the borer extends its dispersion into the southern and western regions.

## DISCUSSION

PAUL DEBACH. How does one conclude from a parasitization of 25 percent, for example, that this results in a certain degree of host population reduction?

W. A. BAKER. Specifically, we know of no method today within the range of our facilities that will permit a quantitative appraisal of the effect of 25 percent parasitism on European corn borer populations.



# Prominent Features of Parasitism of Twig-Infesting Larvae of the Oriental Fruit Moth, *Grapholitha molesta* (Busck) (Lepidoptera: Olethreutidae), in Ontario, Canada<sup>1</sup>

By H. R. BOYCE<sup>2</sup> and G. G. DUSTAN<sup>3</sup>

## INTRODUCTION

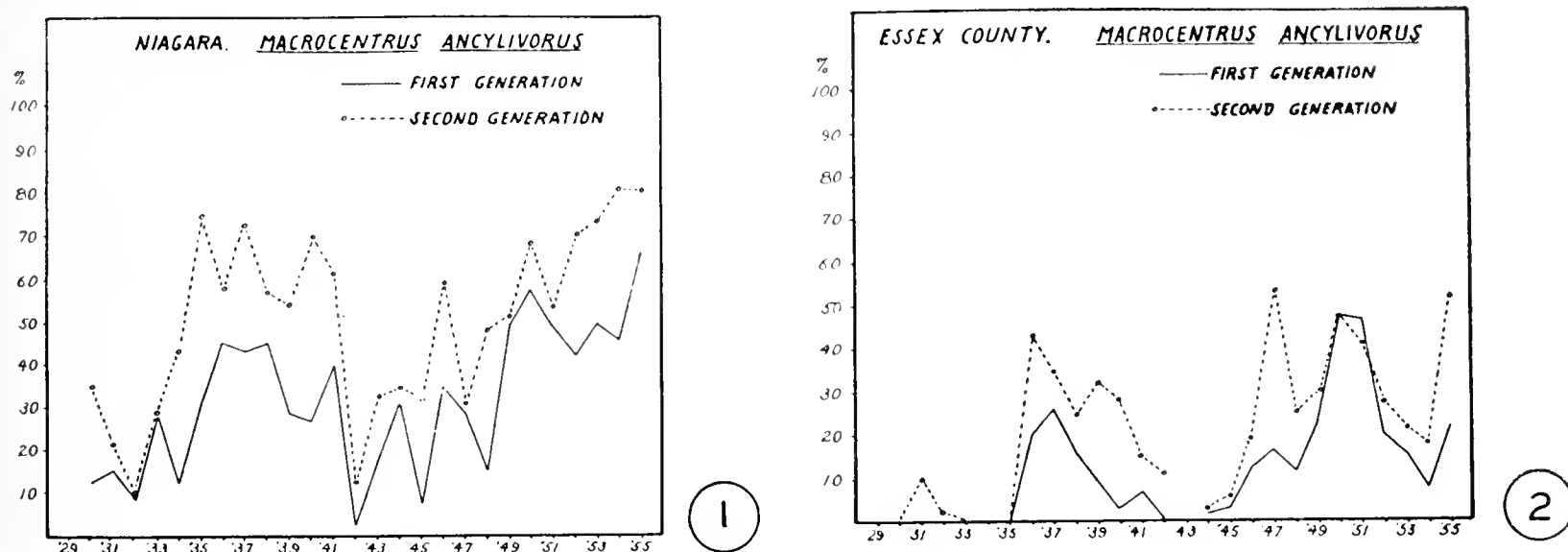
The oriental fruit moth, *Grapholitha molesta* (Busck), was first discovered in the Niagara Peninsula in the autumn of 1925 and, according to Smith (1929), it probably was introduced into the area two or three years earlier. It rapidly became a serious pest of peach in the Peninsula and in Essex County, the two major peach-growing areas of Ontario.

Smith (1929) and Steenburgh (1929) reported that parasitism of *G. molesta* by native species was very low from 1925 to 1928. Steenburgh (1929) suggested that adaptation of native parasites to *G. molesta* was slow and that little control by them was to be expected for a number of years. Accordingly, samples of larvae of the oriental fruit moth and of the strawberry leaf roller, *Ancyliis comptana fragariae* (W. & R.), were collected in New Jersey, U.S.A., during 1929 and 1930 to obtain the braconid parasite, *Macrocentrus ancyliivorus* Rohw., for colonization in Ontario.

Since 1929 the extent of parasitism of twig-infesting larvae of the oriental fruit moth in two- to five-year old peach orchards has been determined annually by methods described by Boyce (1947). Several papers on the results have been published, the most recent being by Boyce and Dustan (1953). They showed that in most years, *M. ancyliivorus* and the native species, *Glypta rufiscutellaris* Cress. were the only parasites of major importance. These data, and those obtained since 1953, show three points of major interest, namely, (1) earlier establishment and generally higher parasitism by *M. ancyliivorus* in the Niagara Peninsula than in Essex County; (2) the dominance of *M. ancyliivorus* over *G. rufiscutellaris*; and (3) the failure of DDT and parathion, as used in peach orchards for insect control, to reduce the degree of parasitism by *M. ancyliivorus*, and the apparently drastic effect of DDT, and possibly parathion, on *G. rufiscutellaris*.

## ESTABLISHMENT AND PROGRESS OF *M. ANCYLOVORUS*

The records of colonization of *M. ancyliivorus*, by means of introductions from New Jersey, by laboratory-reared stock, and by the release of specimens collected in Ontario, are given in Table I. Steenburgh (1930) reported that *M. ancyliivorus* became well established and distributed over an area of approximately 35 square miles in the Niagara Peninsula in 1929, the first year of its introduction. Its subsequent progress, as shown in Fig. 1, was highly successful in this area.



Figs. 1-2. Per cent parasitism by *M. ancyliivorus* of twig-infesting first and second-generation oriental fruit moth larvae, 1929-1955. 1, Niagara Peninsula; 2, Essex County.

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However, it is quite evident in Fig. 2 that in Essex County the initial small releases of the parasite in 1930 and 1931, shown in Table I, were inadequate for its permanent establishment. The extensive colonization of *M. ancyliivorus* in Essex County in 1936, 1937, and 1939 produced a marked increase in its abundance which, however, was not maintained. By 1944 the parasite had reached extremely low levels, and a marked increase did not again occur until after the large scale colonizations in 1946 and 1947. In addition to the number and size of the releases, the difference in the concentration of peach orchards in the two areas may have had a considerable effect on the establishment and dispersal of the parasite. In the Niagara Peninsula, where *M. ancyliivorus* has been more successful, most of the fruit growing area has been closely planted with orchards, particularly of peach, for many years. In Essex County peach orchards were few and scattered in the early 1930's, although their area and concentration has increased greatly since then.

Factors other than the degree of colonization and the concentration of peach orchards have naturally influenced the yearly fluctuations of the parasites in the two

TABLE I—Numbers of *M. ancyliivorus* Rohwer Colonized in the Major Peach-Growing Areas of Ontario, 1929 to 1947.

Year	Niagara Peninsula	Essex County
	No. <i>M. ancyliivorus</i> released	No. <i>M. ancyliivorus</i> released
1929*	2,350	
1930	10,573	94
1931**	3,618	118
1932	4,251	—
1933	1,331	—
1934	4,090	—
1935	16,247	—
1936	—	6,692
1937	—	2,204
1938	—	902
1939***	428	2,128
1940	1,486	137
1941	—	—
1942	—	—
1943	1,288	378
1944	586	—
1945	1,893	—
1946†	—	27,434
1947††	—	7,110
TOTALS	48,141	47,197

\*Material introduced from New Jersey, U.S.A. in 1929 and 1930.

\*\*Parasites from recovery collections and laboratory stock reared on oriental fruit moth.

\*\*\*Parasites from recovery collections returned to orchards 1939 to 1945.

†Parasites reared in the laboratory on the potato tuberworm, *Gnorimoschema operculella* (Zell.) for releases of 1946 and 1947.

††Mated females only released.

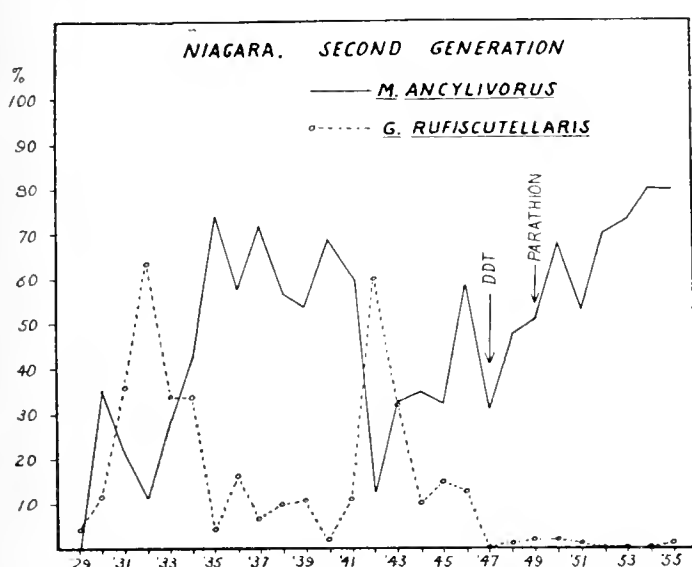
areas although their exact nature and relative importance are not known. However, there is some evidence that the length of time peach twigs remain succulent and support the host larvae has an effect on the population of *M. ancyliivorus* by reducing the size of the overwintering generation. Van Steenburgh (1935) asserted that the decrease in parasitism of the first generation in 1934 was due to the dry summer of 1933 which caused early hardening of twigs and few host larvae were left in feeding locations where they could be reached by the parasite. Additional supporting evidence is found for the years 1942, 1945 and 1948, when, as shown in Fig. 1, parasitism by the first generation of *M. ancyliivorus* in the Niagara Peninsula was 2.6, 7.7, and 14.9 per cent respectively, well below the 26-year average of 31.4 per cent. In the year preceding each of those mentioned peach twigs hardened earlier than usual in July and infested twigs were unusually scarce. Also, in 1941 a heavy rain after a period of drought caused excessive gum formation in injured twigs, resulting in a considerable mortality of second generation host larvae.

In Essex County also there is some evidence that, when peach twigs harden earlier than usual, parasitism of first generation larvae in the following year is comparatively low. This may explain in part the progressive decrease in parasitism from 1952 to 1954, as twigs hardened early in each of the years from 1951 to 1953. By contrast, twigs remained succulent longer in 1948, 1949, and 1950, each of which preceded a year of comparatively high parasitism by *M. ancyliivorus*.

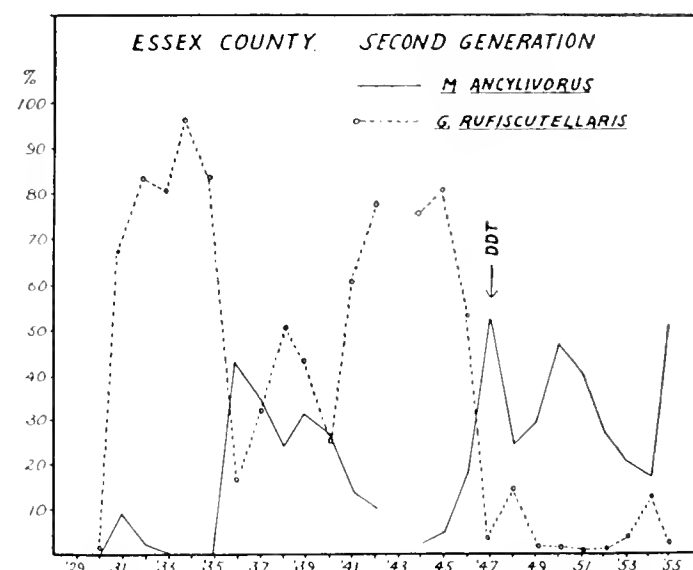
The time and amount of rainfall in relation to temperature probably are largely responsible for the early or late hardening of peach twigs, but so far, except for a few years of extreme conditions, no consistent relationship between rainfall and temperature and twig hardening has been found.

### COMPETITION BETWEEN *M. ANCYLIVORUS* AND *G. RUFISCUTELLARIS*

Van Steenburgh (1934) reported that *M. ancyliivorus* was the dominant species of parasite of the oriental fruit moth in Ontario and that as it increased in numbers *G. rufiscutellaris* became less successful. This inverse ratio of abundance has occurred every year since *M. ancyliivorus* was introduced as is clearly indicated by the percentages of parasitism of the two species plotted in Figs. 3 and 4. In the Niagara Peninsula, where *M. ancyliivorus* has been well established for the past 26 years, the correlation coefficient for the relative abundance of the two species is  $-0.77$ , which is highly significant at the 1 per cent level. Until 1948 this inverse ratio was due to direct competition between the two species, but subsequently their relationship was influenced by the use of insecticides.



3



4

Figs. 3-4. Per cent parasitism of second-generation twig-infesting oriental fruit moth larvae by *M. ancyliivorus* and *G. rufiscutellaris*, 1929-1955. 3, Niagara Peninsula; 4, Essex County.

### RELATIONSHIP OF DDT AND PARATHION TO PARASITE ABUNDANCE

Smith and Driggers (1944) reported that, under cage conditions at least, DDT was toxic to the adults of *M. ancyliivorus*. In a replicated field experiment in Essex County in 1954 it was demonstrated that when a DDT spray was applied to peach trees four days after the peak abundance of the first generation adults of the oriental fruit moth, parasitism of the second generation larvae by *M. ancyliivorus* was significantly lower than where DDT was applied four days before the peak of abundance, the percentages of parasitism under these two conditions being  $43.4 \pm 12.4$  per cent and  $6.7 \pm 6.7$  per cent respectively. However, despite this evidence of toxicity, Boyce and Dustan (1953) were able to report that the general use of DDT in peach orchards in Ontario since 1948, and also parathion in the Niagara Peninsula since 1949, has actually been accompanied by an increase in parasitism by *M. ancyliivorus*. They showed that the average parasitism of the first and second generations by *M. ancyliivorus* was 16.4 per cent and 33.5 per cent in Essex County and the Niagara Peninsula respectively for the 8-year period before DDT was used, and 25.7 and 51.1 per cent respectively in the two areas from 1948 to 1953 inclusive, during which time DDT or parathion, or both were used.

The fact that parasitism in Essex County of the second generation of twig-infesting larvae of the host varied directly with parasitism of the first generation from 1948 to

1955, with the possible exception of 1951, further suggests that DDT applications do not markedly affect parasitism of second-generation larvae. If DDT were causing a serious limiting effect on parasitism of the second generation, which might be expected as a result of the recommended timing of spray applications, parasitism would be expected to be depressed below that of the first generation, and recovery to a high level such as occurred in 1955 might be prevented. Also, comparison of second-generation parasitism in the few unsprayed orchards available with that in sprayed orchards has failed to reveal higher levels of parasitism by *M. ancyliivorus* in the former.

The same general condition also prevails in the Niagara Peninsula where DDT, parathion, or both are applied most commonly at the time when the second generations of the host and parasite are active.

The data plotted in Figs. 1 and 2 show that *M. ancyliivorus* continued its high rate of parasitism in 1954 and 1955, especially in the Niagara Peninsula, despite the continued widespread use of DDT and parathion in peach orchards.

It is not known how the parasite escapes the toxic effects of these two insecticides, one or both of which are usually present on peach foliage when adults of the second generation of *M. ancyliivorus* are present in large numbers. In some orchards in the Niagara Peninsula one or the other of these sprays is also applied when first generation adults are present.

There is no evidence that *M. ancyliivorus* has developed an adaptive strain resistant to DDT or parathion in Ontario orchards, since parasitism was at approximately as high a level immediately following their use as it was seven years later.

The data in Figs. 3 and 4, especially that for the Niagara Peninsula, indicate strongly that DDT and parathion have a detrimental effect on *G. rufiscutellaris*. It will be noted that this parasite has been at a relatively much lower level during the period of *M. ancyliivorus* abundance coinciding with the use of DDT and parathion since 1948, than during the former period of abundance of *M. ancyliivorus* from about 1934 to 1941.

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## DISCUSSION

G. G. DUSTAN. Further work in 1956 showed that *Macrocentrus* was very susceptible to dieldrin in orchards. The parasite from dieldrin-sprayed material developed to the adult stage, but died without leaving the cocoon.

# The Natural Control Complex Affecting Grasshoppers in the Dry Belt of British Columbia

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## ABSTRACT

On the elevated grasslands of central British Columbia where 16 species of grasshoppers commonly occur, two species, *Camnula pellucida* (Sc.) and the complex known as *Melanoplus mexicanus mexicanus* (Saus.), form periodic outbreaks. Of the factors that affect these insects, climate rarely influences them severely; early autumn frosts kill *pellucida* and hot, damp weather favors the fungus, *Empusa grylli* (Pres.), that sometimes wipes out this species but neither frost nor fungus much affect *mexicanus*. Eggs of grasshoppers are attacked by larvae of the meloid beetle *Epicauta oregana* Horn, by *Eutrombidium* mites and rarely, by *Scelio* wasps. *Tachysphex* wasps provision their burrows with nymphs. The best control factors are *Sarcophagidae* of which 14 species parasitize nymphs and adults and sometimes control outbreaks; in turn, fly larvae inside grasshoppers are attacked by two species of the chalcid *Brachymeria*, and puparia, by two *pteromalid* wasps, g. *Nasonia*. Adult flies are caught by *bembicid* wasps and *asilid* flies. Six species of birds especially crows and blackbirds, feed largely on grasshoppers; nestlings of these birds are attacked by seven species of *Protocalliphora* larvae; the puparia of these flies are parasitized by *Nasonia*. Larvae of the *nemestrinid* *Trichopsidea clausa* (O.S.) parasitize *C. pellucida*, sometimes heavily, but seldom *Melanoplus*. Two species of *Tachinidae* attack grasshoppers occasionally. *Bombyliidae* have never been found attacking any stages of grasshoppers although these flies are so important in other parts of Canada. Only once were *gordiids* found, in *C. pellucida*.

The Dry Belt of British Columbia lying between the 49th and 53rd parallels is an elevated peneplain of 2500 ft. to 5000 ft. above sea level, deeply intersected by rivers lying from 500 ft. to 2000 ft. below the level of the surrounding country (Tisdale, 1947). The plains extend for some 5000 square miles and are eminently suited for grazing; the hills rising from the plains are covered with Douglas fir, *Pseudotsuga taxifolia* (Lamb) Brit., and lodgepole pine, *Pinus contorta* Doug. var. *latifolia* Engelm., and in the ecotone between conifers and plains extends in most places, a narrow belt of trembling aspen, *Populus tremuloides* Michx. The elevation of tree line varies in different areas but averages 3000-3500 ft. Large valleys of rivers are terraced by the action of ancient glaciers, and many small valleys contain small streams and swamp vegetation. The precipitation varies from 7 to 10 or 12 inches per year, and summer temperatures range from maximum 95° to 100°F., down to -35°F. in severe winters. The original vegetation (Spilsbury and Tisdale, 1944) was largely awned and awnless bunchgrass, *Agropyron spicatum* Pursh and *inermis* Heller, but increasingly heavy grazing by domestic animals has wiped out this grass over very large areas, to be followed by secondary grasses like three species of speargrass, *Stipa* spp., and finally by brome grass, *Bromus tectorum* Linn. and ruderals.

Some 50 species of grasshoppers, (Treherne and Buckell 1924) live in this zone, subject to cyclic fluctuations of from seven to ten year intervals when from two to five or six species reach outbreak proportions. Heavy overgrazing has so altered vegetation that grasshopper species, once rare or uncommon, now find conditions suitable for increase, and form outbreaks. Where grazing is regulated by fencing large areas and using them in rotation, much of the original vegetation has returned.

In current usage, locusts are grasshoppers that periodically migrate in vast swarms from their place of origin, sometimes for hundreds of miles; grasshoppers are adult insects with wings that do not migrate for long distances so all our native species are grasshoppers; the young of all species are called nymphs. In most populations of these insects in our dry belt except towards the end of the season, both adults and nymphs of several species occur all together; to describe this mixed population of acridiids and tettigoniids of all ages and of several species, the word *groppe* will be used in the following pages.







Considering this chart: the eggs, laid in pods in the ground, are occasionally parasitized by the minute wasps Scelionidae of which one unnamed species of *Scelio* has been reared from eggs of *mexicanus* and a larger unnamed wasp, genus *Sparasion*, occurs in numbers on some ranges and is probably parasitic upon eggs of the tettigoniid *Anabrus longipes* Caudell. The meloid beetle, *Epicauta oregana* Horn, occurring some years in vast swarms, drills holes in the ground and lays eggs therein in areas of heavy *pellucida* nymph population in alkaline soil where these same grasshoppers will oviposit a month hence. Larvae of these beetles have been recovered from egg beds where they had destroyed many egg pods. The adult beetles feed upon alfalfa and snowberry, *Symphoricarpos racemosus* Mich. and are often pestered continuously by hordes of minute ceratopogon midges, *Atrichopogon* (*Melochelea* sp.), which feed on the yellow oily secretions oozing from thoracic segments and more especially from femorotibial joints. Carabid larvæ have also been found eating egg pods. None of these except the meloid larvae are of much more than interesting occurrences.

On groppers themselves both nymphs and adults, a wide range of creatures feed. On the wings of adults, nymphal *Eutrombidium* mites sometimes attach in great numbers, which vary according to the species of host: thus on 100 *pellucida* counted, there were 57 mites and on 100 *mexicanus* taken at the same time, same place, were 360 mites; other species of groppers had very few. Sometimes the meta-wings are red with mites clinging for the most part to the veins of the vannal area. Adult mites are reported to feed on gropper eggs; this has not been observed so far on these grasslands.

The fungus, *Empusa grylli* (Fres.), not infrequently wipes out populations of both nymphs and adult *pellucida* in areas of heavy vegetation but only when conditions are warm and moist. Infected insects climb up weeds or grass heads to which they cling with the first two pairs of legs, the meta-legs stretched out, and there die: the head and sometimes the thorax, turns white. As many as 9 and once 13 fungus-killed insects have been counted on one plant head. When conditions are right, *E. grylli* is extremely effective but only on *pellucida*; other species are virtually immune.

Mammals, birds, insect predators and insect parasites all play their part in reducing gropper populations; some are of merely academic interest but others are very effective.

Of mammals, coyotes, *Canis latrans lestes* Herr., and to a lesser extent wolves, *C. lupus* Linn., feed singly and as families on groppers at dusk, pouncing upon them with their front feet. Horses, cattle and sheep play a very important but unconscious role in gropper destruction when they move over the ranges, disturbing the insects and causing them to fly, when parasitic sarcophagid flies larviposit upon them; these flies cannot larviposit on sitting groppers so anything that makes them fly, especially these domestic animals, are important aids in control.

Numbers of birds feed part time or continuously on groppers. Those that occur in huge flocks like crows and blackbirds remove enormous numbers in a day; the crop of one crow, *Corvus brachyrhynchos* Brehm, examined in Upper Hat Creek by Dr. R. D. Bird, contained 27 groppers and since crows feed many times a day and occur in flocks of from 50 to 1000 birds in summer and early autumn, their effect is very great. Brewer's blackbirds, *Euphagus cyanocephalus* (Wagler), flock in thousands and clean out groppers in an area; the flock literally rolls along, the birds at the back leap-frogging over the main flock and settling ahead. In one area where the population of groppers had just been estimated to be 18 per square yard, a vast flock of blackbirds settled and a count taken immediately behind them, yielded one insect per 7 and 9 yards. Sparrowhawks, *Falco sparverius* Linn., sit on rocks or fence posts and feed all day on groppers, generally first pulling off the head, hind legs and crop. Meadow-larks, *Sturnella neglecta* Aud., robins, *Turdus migratorius* Linn., bluebirds, *Sialia currucoides* (Bechstein), and grouse, *Pedioecetes phasianellus* (Linn.), feed continuously on these insects. In turn, nestlings of these birds (except hawks and grouse which have not been examined) are attacked sometimes very heavily, by larvae of six or seven species of *Protocalliphora* which live in the substance of the nests and suck blood from nestlings; in some years their attacks are fatal to the nestlings. The larvae of at least one species, *P. hirudo* S. & D., feed inside the birds and always kill them. In turn, the puparia of these flies are often attacked 100 per cent, by the minute pteromalid

wasp, *Nasonia* (*Mormoniella*) *vitripennis* (Wlkr.), of which as many as 18 to 41 may develop in one puparium; no flies ever emerge from puparia parasitized by these wasps.

Of insect predators, the very large asilid fly, *Stenopogon inquinatus* Lw., catches adult grasshoppers in flight, drops to the ground and sucks out their blood. Adult grasshoppers are also caught, stung and paralysed by the big wasp, *Priononyx* (*Sphex*) *pudidorsus* (Costa) (= *Chlorion bifoveolatum* Fernald), which drags its prey laboriously through the grass and shoves it into a tunnel as food for its grub. Other hunting wasps which do this are species of *Tachytes*, and *Tachysphex tarsatus* (Say) which catch immature acridiids usually of the third instar. *Tachysphex* especially is in turn followed by two metopiid flies, *Euaraba tergata* Coq. and *Taxigramma heteroneura* Meig., which follow the wasp dragging its prey, wait until the hopper has been inserted into the tunnel and the wasp has come out for a few seconds rest, then dart in and deposit a living maggot on the hopper. One female *E. tergata* imprisoned in a vial, deposited 24 living maggots before dying; each maggot was encased in a tubular membrane which extended only half-way up its 1 mm.-long body and from which the maggot immediately wriggled free. These maggots were inserted into minute cuts made in the intersegmental membranes of small nymphs of *pellucida*, *mexicanus* and *Amphitornus coloradus ornatus* but they all wriggled out again and would not remain in the nymphs' bodies. Others placed on the surface of immobilized nymphs made no effort to burrow in. It is possible that the maggots need to eat the wasps' eggs first and then the paralysed nymphs and cannot feed on living food.

The most important, most widespread and most effective natural control factors of groppers in British Columbia are 15 species or varieties of sarcophagid flies which we have reared from their hosts. These are:—*Blaesoxiphotheca coloradensis* (Ald.); *Helicobia rapax* (Walker) (= *helicis* Towns.); *Acridiophaga* (*Sarcophaga*) *aculeata* (Ald.); *A. aculeata* var. *taediosa* (Ald.); *A. a* var. *gavia* (Ald.); *A. aculeata* vars. unknown, females only; *A. falciformis* (Ald.); *A. caridei* (Brethes) (= *angustifrons* Ald.); *Kellymyia kellyi* (Ald.); *Robineauella tuberosa* var. *exuberans* (Pand.); *R. t.* var. *sarracenioides* (Ald.); *R. t.* var. *harpax* (Pand.); *Opsophyto opifera* (Coq.); *Protodexia hunteri* (Hough).

All these flies sit on vantage points in a field such as stones or pieces of dried cow manure, dart at grasshoppers flying by or at late instar leaping nymphs, strike them from above and deposit living maggots upon them. The maggots develop in their hosts, emerge usually through the cervical or post-thoracic membranes and immediately enter the soil to pupate. A single maggot of a large species of fly, as are most of them, invariably kills its host while small maggots as are those of *opifera* do not necessarily kill their hosts unless several maggots are present in the body at one time.

When abundant, these flies cut down a gropper outbreak almost miraculously and the year following there seems to be more flies than groppers, and then the flies die off.

Maggots of most of these flies have been used in rearing experiments by gently squeezing them from the bodies of anaesthetized females and placing them on or in, the bodies of immobilized groppers. Only one species, *K. kellyi*, lends itself readily to artificial propagation because the maggots will develop in a succession of dead grasshoppers supplied to them. The maggots of all other species will not pass from a consumed gropper to another one; this suggests that *kellyi* is normally saprophagous but for some reason suddenly becomes a very active and efficient parasite in the field. Its presence anywhere is very erratic; most years it is not to be found at all.

With sarcophagid maggots the only part of a host's body that is readily penetrated, is the tympanum which a first-instar maggot can penetrate in from 10 to 30 seconds; they are much slower in penetrating intersegmental membranes or fail to penetrate at all and dry up and die.

When inside a host, a maggot feeds on blood, starving first the fat body and then the reproductive organs which shrivel up or never develop at all except the egg calyces which remain large; the malpighian tubules become free of the fat mass and lie free in the body; the salivary glands and digestive system are unaffected until the maggot is

nearly full-grown and is voracious, when it consumes the muscles and digestive tract posterior to the crop, and then emerges. It is remarkable that a gropper with a relatively huge maggot inside it can still walk and hop although it is a mere shell; as soon as a maggot emerges, the host dies.

Predators on these sarcophagid flies are spiders and three species of bembicid wasps of which *Epibembix comata* Park. is the chief one and it in turn is tracked down to its tunnel in the sand by the metopiid fly, *Metopia leucocephala* (Rossi). The only unproved link in this series of food chains is a very common mutilid wasp, *Dasymutilla vesta* (Cress.), which may prey on bembicids but has not yet been shown to do so. Also a predator on these sarcophagids is the asilid fly, *Cryptopogon willistoni* Curran, which has been watched feeding upon *K. kellyi*.

Parasites on the pupae of Sarcophagidae are the pteromalid wasps, *Nasonia* (*Mormoniella*) *vitripennis* (Walk.) and *N. brevicornis* Ashm. Wherever these minute wasps find a muscoid puparium (not larvae) they drill into and lay eggs within the thick pupal wall, apparently leaving behind them an odour indicating that that puparium has been utilized because succeeding wasps make no effort to puncture it. Up to 18 and 27 wasps have been reared from one puparium and from one dissected puparium 4 teneral adults and 37 larvae were taken. The larvae of these parasites are predators, feeding externally on the fly pupa under cover of the puparium and when mature, all emerge through one hole.

The most interesting section of this food chain is what I call the chalcid complex which involves the two chalcid species, *Brachymeria coloradensis* (Cress.) and *B. tegularis* (Cress.). The first species has been recorded several times in literature as being a parasite of several species of grasshoppers; definitely it is not, it is a parasite on the sarcophagid larva within the grasshopper. In very many populations of our grasshoppers, this chalcid has been noted following one particular insect for long periods of time, attempting to settle upon it and being chased away by the grasshopper which eventually seems to tire and then the wasp sits on the cervix or just behind the prothoracic shield and apparently injects an egg into the membrane. In every instance, the grasshopper being chased has been shown to contain a sarcophagid maggot. Grasshoppers that have been attacked successfully by these chalcids have been caged, the emerging sarcophagid maggots allowed to pupate and in every case, chalcids have emerged from the puparia instead of flies. The wasps never make mistakes. How do they know that a grasshopper contains a maggot?

In 1954 the Kamloops ranges carried a fairly heavy gropper population but except for small numbers of only three species of Sarcophagidae, the flies were practically absent. On the other hand, *B. coloradensis* and a few *B. tegularis* were more abundant than I have ever seen them before; scores fed upon every clump of flowers on the ranges and from the very few puparia obtained at the end of the season from hordes of grasshoppers kept in cages, these chalcids emerged in the laboratory, during the winter. An enormous population of chalcids must have built up during 1953 and attacked most of the maggots within the grasshoppers, thus accounting for the scarcity of flies in 1954.

One other wasp, the braconid *Aphaereta auripes* Prov. (= *A. muscae* Ashm.), has been reared from sarcophagid pupae, but it is rare.

Two species of Nemestrinidae, *Trichopsidea clausa* O.S. and *Neorhynchocephalus sackeni* (Will.), are potentially first-rate parasites of *C. pellucida* but are at present at a very low ebb on account of the paucity of their egg-laying sites in poles and dead trees on the open ranges; they are dealt with separately.

The Tachinidae are of little consequence as parasites of grasshoppers in this province. A small species, *Euacemyia tibialis* Coq., has been reared from *M. m. mexicanus*, but only from those occurring in damp depressions and in the edges of woods. For some reason, in 1954 when most sarcophagids were entirely absent, more tachinids were observed amongst groppers in the field than ever before.

Finally in this chain must be mentioned the recovery from only one individual *C. pellucida*, of five gordiid or mermithid worms; the grasshopper was collected on the marshy edge of a large range pond in the Chilcotin. These worms are very common in

acridiids in western Ontario but of the thousands of grasshoppers that have been examined every year in British Columbia, these five worms are the only ones that have been recovered.

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### DISCUSSION

S. D. MISRA. Did you find the plagues of grasshoppers, in general, and *Camnula*, in particular, associated with any particular grass or grasses?

G. J. SPENCER. In general, yes, but it varies greatly. In Saskatchewan *Camnula* does not eat dandelion; at Kamloops it is a favoured food. *Camnula* favours *Poa*, but in dry years of scanty vegetation, it will eat grass stalks and the driest hay. It is not usually a broad-leaf feeder.



# On the Nemestrinidae of British Columbia Dry Range Lands

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## ABSTRACT

Only two nemestrinid flies have been found in British Columbia, *Trichopsidea clausa* (O.S.) found freely as far north as the 52° latitude, and *Neorhynchocephalus sackeni* (Will.) which occurs sparingly in its apparently extreme northern range at 50° 40' latitude. Both species are parasitic on grasshoppers. The fly *T. clausa* oviposits in crevices and in beetle emergence holes in dead trees and fence posts and larvae from these eggs are wind-distributed. They enter grasshoppers through intersegmental membranes and form spiral-walled respiratory tubes arising from large and even very small tracheae. Where a nemestrinid and sarcophagid larvae occur in one host insect, the nemestrinid only survives and ultimately invariably kills its host. The habits and structure of the flies and larvae are described and the ecology and economic importance of the species are discussed.

On the elevated grasslands of the Dry Belt of British Columbia where several species of grasshoppers form outbreaks or are present in large numbers practically every year, two species of nemestrinid flies occur, *Trichopsidea* (*Parasymmictus*) *clausa* (O.S.) which occurs freely as far north as the 52° parallel, the furthest north of any fly of this family in the world, and *Neorhynchocephalus sackeni* (Will.) which reaches its northern limit on latitude 51° where it occurs very sparsely. On the northern ranges the flies occur up to 3200 ft: in the southern (Nicola) ranges, up to 4000 ft. Both species of flies somewhat resemble honey bees, are covered with long golden hair and are very much alike except that *sackeni* has a long proboscis while *clausa* has a very short but quite functional proboscis.

Both these flies are parasitic upon grasshoppers; in this province at least, *clausa* is restricted almost entirely to *Camnula pellucida* Scudder and *sackeni* to the complex of species currently called *Melanoplus mexicanus mexicanus* (Saussure). The species *clausa* was first reported from the Chilcotin, Cariboo country in 1929 (Spencer, 1931) and *sackeni* was first found at Kamloops in June 1943 by E. R. Buckell and reared from *mexicanus* in 1945.

My work on them was done at intervals between 1929 and 1940 as one phase of a study of the bionomics of range grasshoppers in the Chilcotin and Kamloops-Nicola areas for the Federal government and for three months in 1954 under a research grant from the University of British Columbia; details of structure were worked out at the University. Initial short notes on them were published by Spencer (1931, 1932, 1945). They have been studied in Montana and well written up by York and Prescott (1952) and by Prescott (1955); a thorough study on a very similar species in the Argentine was made by De Crouzel and Salavin (1943).

A great deal of my findings on behaviour and structure of these flies parallels and agrees with that of Prescott and York and of DeCrouzel and Salavin and therefore will not be repeated here: I shall include only features that these workers have not touched on.

Since *sackeni* is so rare in British Columbia, very little work has been done on it; most of the following is descriptive of *clausa*. This species lays eggs in cracks in dead trees but especially in the smooth-sided emergence holes of buprestid beetles that are to be found in most fence posts and telephone poles on the ranges. In long lines of poles, the flies oviposit only in those which run through or are closest to, egg beds and high nymphal populations of *Camnula*; poles outside of these population areas are not utilized. An immense number of eggs, up to 4000 each, is deposited by a female at the rate of 30 eggs per 35 seconds in the Kamloops area and considerably slower further north. When a pause occurs, the fly shifts her ovipositor slightly and resumes egg-laying for another 35-second-or-so period. The flies appear first about mid-June in most years and are scarce or absent by the 10th of July.



Male flies have never been taken in the field at the same time as ovipositing females; less than a dozen in all have been found and then only in upland flower meadows, around dusk, on yarrow *Achillea millefolium* Linn. and geranium flowers *Geranium viscosissimum* F. & M. Only once has a pair ever been found in coitu, on a flower in a meadow at 3300 ft. Whether the sexes mate on the ranges and males then fly up to the meadows or whether males depart for the meadows as soon as they emerge from pupal cases and the females go up to the flower meadows to mate and descend to oviposit, has not been determined.

During the last 15 years the Kamloops ranges where these studies were made, have been taken over by sheep farmers who have removed fence posts over 50 square miles of grazing land, leaving no oviposition sites for the flies. In 1954, many flies were on the ranges hunting for oviposition posts among grasshopper populations, even alighting on human beings and on the vertical boom of a spraying machine. Therefore ten fence posts were erected at strategic places and heavily punched with an oval spike to leave holes simulating those left by emerging buprestid beetles. Those hammered into solid wood were occluded in a day or so by inwardly projecting wood fibres and were found to be rejected by ovipositing flies but those in soft or semi-rotten wood had smooth walls and were readily accepted by flies. Moreover, rain tended to close up these punched-in holes; those drilled out, although circular, have smooth walls, do not close up in rain and are acceptable for egg-laying.

Flies must hunt locations by sight because fence posts even in the process of being erected, were visited by as many as 9 and 11 flies at a time. Irrespective of the time of day, egg-laying does not begin until an air temperature of 65°F. in the shade, has been reached: flies that have spent the (cold) night on posts, remain quiet until that temperature prevails when they promptly begin to lay. They have a tendency to remain quiescent in calm weather; wind is a direct stimulus to oviposition. When tested with an anemometer, it was found that wind with a minimum velocity of 2.74 miles and up to 3 m.p.h. was enough to start egg-laying which was continued even when the wind reached 15 miles per hour.

The ovipositor of a female consists of two, 4-6 mm-long valves which are slightly enlarged and divergent at the tips. To discover the location of an oviposition stimulus, all parts of the abdomen of a quiescent fly were touched very gently with the tip of a vibrissa of a mouse, mounted in a holder, with no result until the inner surface of the divergent tips of the ovipositor were touched, when the trembling egg-laying movements started at once. This is apparently the stimulus that is supplied by wind to the ovipositor.

The eggs of both *clausa* and *sackeni* are elongate, slightly curved, pointed at both ends and are held together and to the substrate by a weak cement which disappears when the eggs hatch. Clumps of eggs up to 30 at a time, are sometimes carried off by the ubiquitous ant *Lasius niger* whose food-hunting hordes may practically strip a post of its eggs.

The egg-laying habits of *sackeni* in British Columbia are still in doubt. Only twice have females been taken when they were hovering over seed heads of grasses, making continuous stabbing movements at the grass heads with ovipositors directed forwards under the abdomen, giving every appearance of laying eggs. While doing this their wings emitted a very high-pitched note which betrayed their presence even when the flies could not at first be seen. Grass heads that had been stabbed at were examined very carefully but no eggs could be found on them. York and Prescott (1952) state *sackeni* oviposits in holes as *clausa* does; this has not been seen on our ranges. The two females that seemed to be ovipositing on seed heads were confined in a large glass jar with grass seed heads, in the laboratory. One soon died although it was heavily gravid but the other laid eggs all over the grass heads and also on the sides of the jar. The eggs were laid on July 15, started hatching at midnight on August 2 and by 5:30 p.m. August 3 had almost all hatched after an incubation period of 18 days.

The behaviour of first instar larvae of both *clausa* and *sackeni* is identical. In both cases the 1 mm.-long maggots (Fig. 1) may remain motionless for hours at a time or crawl slowly or loop like geometrid caterpillars or sit upon six 0.12 mm.-long spines

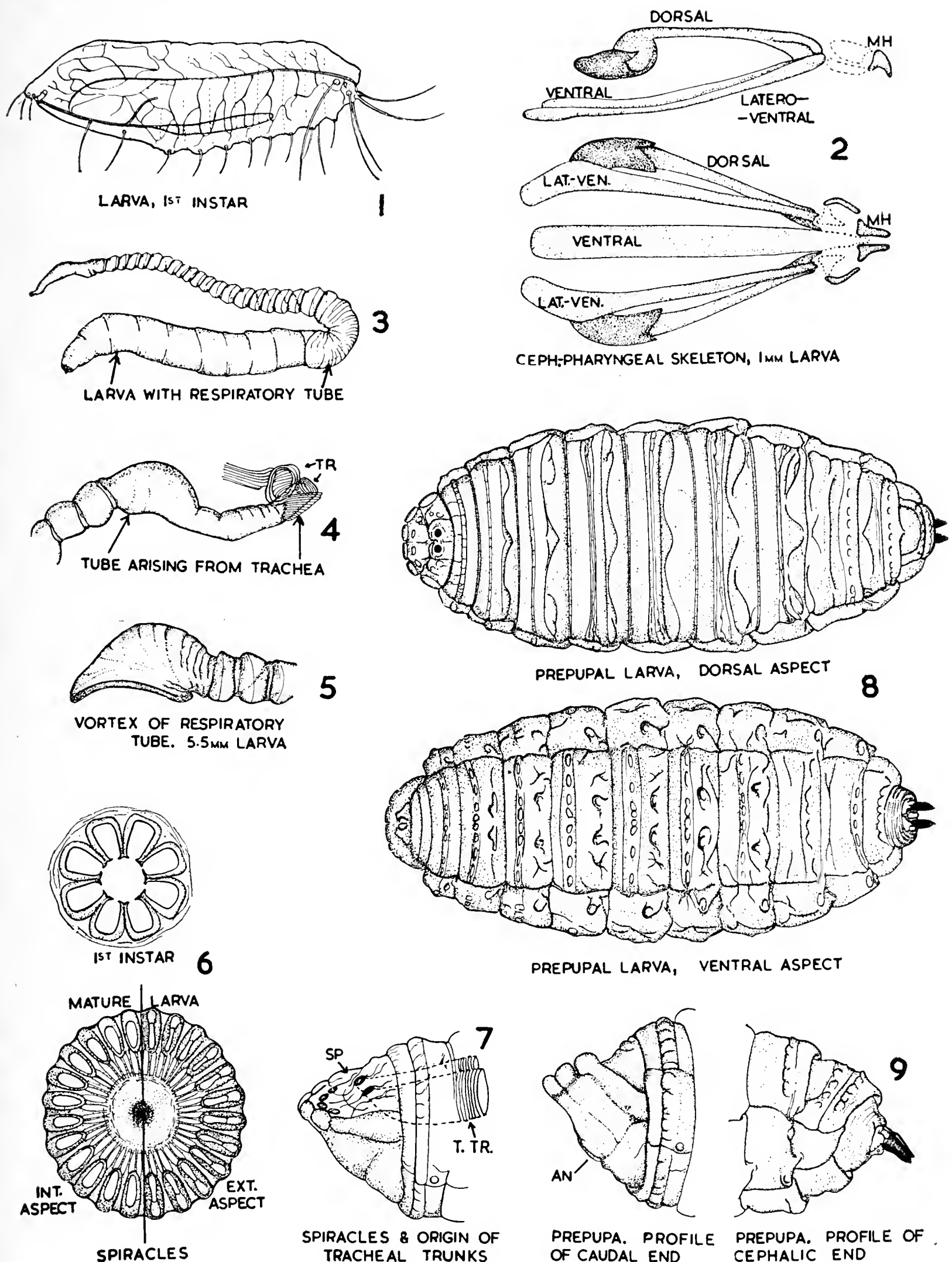


Fig. 1. Larva, 1st instar, showing salivary gland, tracheal trunk and long setae. Fig. 2. Cephalopharyngeal skeleton of 1st instar larva. Fig. 3. Half-grown larva with spiral respiratory tube. Fig. 4. Origin of tube from a small trachea. Fig. 5. Vortex of tube which envelopes caudal end of larva. Fig. 6. Spiracles: *Upper*, 1st instar larva. *Lower*, spiracle of mature larva; right half, external aspect; left half, internal aspect. Fig. 7. Profile, caudal end of mature larva. Spiracular declivity and 4 oval truncate projections which are absent in *N. sackeni*. (See also Fig. 13). Fig. 8. Dorsal and ventral aspects of mature, prepupal larva. Fig. 9. Left figure, prepupal larva, profile of caudal end showing anus = an. Right figure, profile of cephalic end showing pointed mouth hooks.

on the caudal end of the body, either motionless or swaying from side to side. When a wind of a certain velocity strikes them they flip their bodies into the air; when egg masses are hatching from posts, the larvae are carried by the wind and scattered over

surrounding territory. This reaction has often been tested by using a glass pipette and blowing at various speeds into a jar containing larvae and also at eggs hatching on posts. A gentle current stimulates them to waving from side to side, but when it becomes stronger they hurl themselves about; when in the jar they stick to the sides wherever they hit as they probably stick to grasshoppers if they should happen to strike them. It was not possible to register the speed of the jet necessary to cause larvae to jump, on the anemometer available. Out of doors, all eggs in any mass hatch at the same time and the maggots are almost immediately blown away. Eggs hatch at a threshold temperature of 61°F. and larvae are quiet at 56°F. but respond to warming up air by slight activity: gusts of from 3-5 m.p.h. make them leap but the threshold speed could not be determined.

Many experiments have been performed to discover how these minute and delicate maggots enter grasshoppers. Prescott (1955) has shown that *sackeni* enters sclerites on the mid-lateral line near spiracles, leaving a black mark at the point of entrance. Both species of larvae form respiratory tubes (Figs. 3,4,5) starting, in *clausa*, from tracheal trunks or remarkably small tracheae almost anywhere in the thorax and abdomen but not from air sacs, and in *sackeni* from the small black entrance marks. In this province these black marks have been found only twice out of thousands of grasshoppers that have been examined, so it has not been possible to determine what happens if a *sackeni* larva infests a late instar nymph and the nymph moults to an adult. Is a new respiratory tube formed or a new connection made with the body wall? These tubes are of broad continuous spiral bands and end in a smooth membranous vortex which envelops the posterior end of the larva (Fig. 3) enabling it to breathe from a trachea, or from outside the body wall in the case of *sackeni*.

To determine how these larvae enter their hosts and form these tubes, I have immobilized adult grasshoppers and larger nymphs of the seven commonest acridiids on the ranges but chiefly *C. pellucida* and *M.m. mexicanus* with thin strips of adhesive tape across the body and metalegs and have placed on them from 1 to 12 to 30 and up to 50 larvae at a time, of both species of flies, carefully transferring each one with the delicate tip of a mouse vibrissa. They have been placed at different times of the day, from cervix to caudal end of male and female grasshoppers either generally distributed or localized systematically dorsally, laterally and ventrally along body segments, on spiracles and on tympana. Most larvae crawl slowly over the grasshoppers, some die without moving, some crawl between segments and others shrivel up and die. The only place where they have been seen entering is at the base of the cerci and under the pronotum; they cannot enter abdominal spiracles, and get squeezed by the opening and closing mechanism of thoracic spiracles. Now sarcophagid larvae enter tympana faster and more easily (in from 10 to 30 seconds) than anywhere else but not so the nemestrinid larvae which seem unable to enter a tympanum. After exposures to these maggots of several hours to overnight, the grasshoppers have been caged separately and kept until they died naturally or killed after two or three weeks, and then dissected; not one maggot has ever been recovered even in those cases where they were seen to enter at the base of cerci.

Very careful caustic potash and whole mount preparations of first instar larvae of *clausa* show two relatively very large salivary glands (Fig. 1) extending nearly the whole length of the body, their ducts uniting anteriorly and leading to the ventral sclerite of the cephalo-pharyngeal skeleton. In all older larvae these glands are very much smaller. It is possible that their secretion is necessary to small larvae for softening the body wall of their hosts during penetration and that larvae enter most successfully through intersegmental membranes.

Whole mounts also show a smooth inner cuticle underlying the setaceous one of first instar larvae indicating that they either moult in the act of penetrating their hosts or immediately afterwards. Their very small size and transparency accounts for the fact that none has ever been located in a grasshopper: the smallest one I have found was 2.5 mm. and was already provided with a breathing tube.

The respiratory tube is probably formed in the same way that Beard (1942) showed that the tracheal funnel of the larva of the tachinid fly *Trichopoda pennipes*

Fab. that parasitizes the bug *Anasa tristis* Deg., develops from wound tissue of the trachea of the host. Therefore, the nemestrinid larvae must penetrate the tracheal wall backwards and in some way stimulate it to form a smooth envelope around the anal spiracular end of their bodies and to keep on secreting the broad spirally-ringed tissue until the full length of the tube, some 16.2 mm. in mature larvae, is reached (Fig. 3).

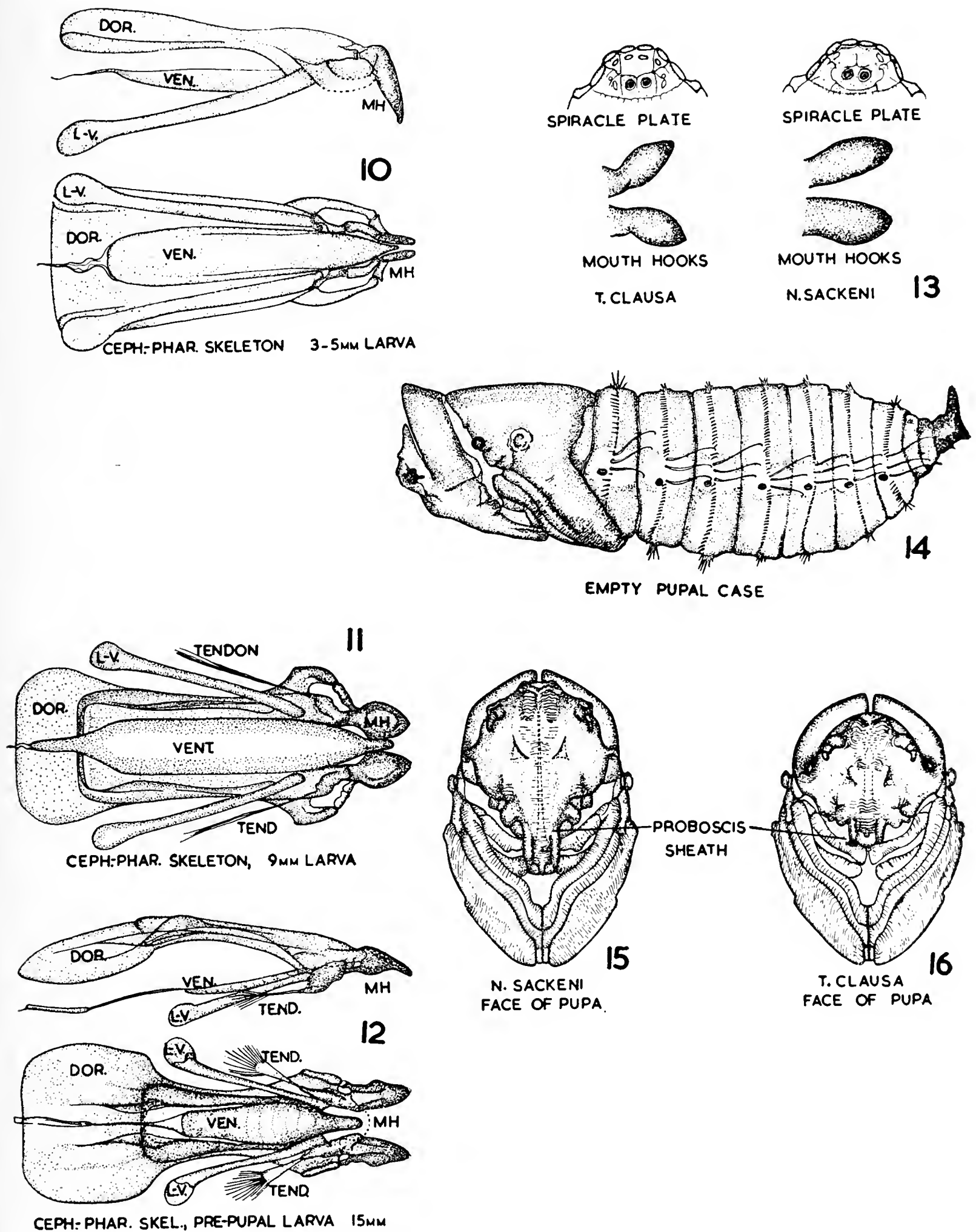


Fig. 10. Lateral (upper) and ventral aspects of cephalo-pharyngeal skeleton of 3 to 5 mm. larval. Fig. 11. Ventral aspect of 9 mm. larva showing beginning of tendons. Fig. 12. Lateral (upper) and ventral aspects of mature, prepupal larva with large tendons and flaring, truncate dorsal plate. Fig. 13. Left side: upper, spiracular declivity of mature *clausa* larva showing 4 oval truncate projections. Lower, (camera lucida) plan of pointed *clausa* mouth hooks. Right side: upper, spiracular declivity of mature *sackeni* larva showing only 2 oval truncate projections. Lower, (camera lucida) plan of blunt *sackeni* mouth hooks. Fig. 14. Lateral aspect, empty pupal case of both *clausa* and *sackeni*. Fig. 15. Frontal aspect of pupa of *N. sackeni* to show long proboscis sheath. Fig. 16. Frontal aspect of *T. clausa* pupa to show short proboscis sheath.



During ecdysis the exuviae must be passed backwards and with the mouth hooks, come to lie in the vortex of the tube (Fig. 5) where it must be absorbed or else it would block the tube. The re-establishment of the caudal end of the recently-moulted and rapidly-growing larva must be a critical performance. The Argentinian workers De Crouzel and Salavin (1943) report that they have commonly found mouth parts of a smaller larva in the vortex; I have examined very many tubes and have found only one set of mouth hooks.

My study and a series of measurements of cephalo-pharyngeal skeletons (Figs. 2, 10, 11, 12) would seem to indicate that these larvae moult four times (a) immediately upon entering a host (b) between the 2.5 mm. size (c) at the 9 mm. size and finally to reach the pre-pupal condition of 15 mm. to 20 mm. at which stage (Fig. 8) they emerge from their hosts, leaving the respiratory tube behind. The final moult to the pupa may be delayed for a long time.

Within their hosts, no two nemestrinid larvae ever live together for long; one only survives. They are also dominant in competition with sarcophagid and tachinid larvae which they invariably destroy. I have found one nearly mature sarcophagid larva, one half grown and one small one, all killed by a *clausa* larva barely 3 mm. long which was obviously the most recent arrival. This is slightly different to the findings of Prescott (1955) in Montana who found nemestrinid and sarcophagid larvae alive together, but nemestrinids mutually antagonistic.

The effect of these larvae on their hosts is to destroy the reproductive organs. In the *female* grasshopper, the terminal part of the egg calyx is shortened, the calyx itself thickened, eggs if mature or nearly mature are reduced to pulp and finally absorbed and if the ovarioles are immature and still developing, they are starved and do not increase beyond embryonic size. The fat mass usually but not always, disappears and is reduced to a membrane, the Malpighian tubules tend to lump together and to coalesce: the blood is not depleted until the maggot is full-grown. In the *male*, the testes lose their tubular form and become mushy until they are nearly or quite absorbed. The other organs change as they do in the female.

Although equipped with relatively huge mouth hooks (Figs. 8,9) the larvae ingest only liquid food until mature and ready to leave, when they practically hollow out the host. As nearly as I can determine, the gut is imperforate until the prepupal stage at which the larva emerges from the host.

The larvae leave grasshoppers through the membrane between thorax and abdomen and sometimes through the cervical membrane and at once enter the soil. If the soil is light and friable, they penetrate but come out again almost immediately and may wander round on the surface or be quiescent for over a year, until they shrivel and die. De Crouzel and Salavin (1943) record larvae of a closely related species surviving for nearly three years without pupating. York and Prescott (1952) have shown that the nature of the soil decides pupation; a firm soil enables them to pupate at once; friable soil brings them up again. After the full pupal period, the armature of the pupa enables it to wriggle to the surface where it protrudes, splits open (Fig. 14) and allows the fly to escape.

The similarities and differences between the stages of these two flies are as follows:—

The eggs of both species are alike.

The *larvae* are alike and indistinguishable until nearly mature when they can generally be separated by *clausa* having four, oval flat-topped projections (Fig. 7) on the dorsal, caudal declivity, lying in an arc between the conspicuous round spiracles (Fig. 6) and the end of the body: in *sackeni* the two median projections are absent or all four are absent or merely indicated (Figs. 7,13).

The mouth-hooks of mature *clausa* maggots are more pointed than those of *sackeni* (Fig. 13).

The *pupae* can be separated by the proboscis sheath being long in *sackeni* and short in *clausa* (Figs. 15,16).



In the adults, *sackeni* has a long proboscis and *clausa*, very short mouth-parts entirely concealed by golden hairs. The bodies of both flies are alike in being clothed with long, golden hairs, in the females of both species having 3-4 mm.-long ovipositors, and the males having the abdomens tipped with a blunt spur.

The effectiveness of these two nemestrinid flies has not had a fair trial in British Columbia on account of the paucity or complete absence of posts for egg-laying, in the areas of highest grasshopper concentrations. The highest percentage infestation obtained in any year was 70% on *C. pellucida* whereas in Montana Prescott (1955) has recorded infestations of over 90%. The efficiency of the flies is without question. In 1954 in an area of about 150 yards where only 4 posts had been set out, the parasitism by *clausa* by the 10th and 12th of August ran: *C. pellucida* 41.6% (total parasitism for *Camnula* including sarcophagids, was 46.34%); *Trachyrachis kiowa kiowa* 21%; *Metator nevadensis* 40%; *M.m. mexicanus* 7%; *Amphitornus coloradus ornatus* 0%.

Men at Farmers' Institute meetings and individual cattle and sheep growers have been urged to put out old fence posts without bark and full of cracks and beetle holes, in areas of known *Camnula* egg beds and breeding grounds, as a sure means of keeping down large percentages of several species of grasshoppers but up to the present, this has not been done and this splendid natural control factor has not been utilized.

### ACKNOWLEDGMENT

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# The Evanescence of Perfect Biological Control

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## ABSTRACT

The introduced ladybeetle, *Chilocorus cacti* (L.), proved so effective in totally eliminating the scale insects, *Pseudalacaspis pentagona* (Targioni) and *Asterolecanium pustulans* (Cockerell), from Puerto Rico for twelve to fourteen years that no beetles survived to control new infestations. The giant Surinam toad, *Bufo marinus* (L.), was so effective in eliminating white grubs, *Phyllophaga portoricensis* Smyth and *P. vandinei* Smyth, from the cane fields of Puerto Rico for fifteen years that no toads survived to control incipient new white grub infestations.

"No organism can increase indefinitely as the lack of food is the ultimate check. In nature this ultimated check is seldom reached, as there are nearly always factors preventing it." Thus wrote the veteran Entomologist, Dr. F. A. G. Muir, in his Introduction to Francis X. William's "Handbook of the Insects and other Invertebrates of Hawaiian Cane Fields" (*Hawaiian Sugar Producers' Experiment Station*, 400 pp., illus., Honolulu, 1931). It seems rather surprising that this "ultimate check" was not reached in the Hawaiian Islands, or at least was not noted or recorded by Dr. Muir or the numerous other entomologists there, with their wealth of experience in the importation from abroad of parasites and predators, for in the equally limited insular environment of Puerto Rico, two such occurrences are very conspicuous.

The introduction from abroad of a beneficial parasite or predator is predicated on the assumption that the pest on which it is expected to prey will be somewhat greatly reduced in numbers, but not that it will absolutely disappear, and subsequently result in the elimination of the parasite or predator. That is: control is anticipated at most to be 85 or 90 or 95% effective of the pest, but not 100%. Commercially effective control is preferable to so close an approach to perfection that the beneficial parasite or predator starves to death from lack of food, and years later the pest reappears in overwhelming abundance, with no natural check for its control.

In the first few years after the establishment of the experiment station at Río Piedras (1910), the rows of bucayo trees, *Erythrina glauca* Willd., from its entrance leading out to the main road, each fall were defoliated by mass infestations of the soft, greenish-brown scale, *Pulvinaria psidii* Maskell. As the female scales mature, their bodies are pushed off the host by the accumulation of eggs, and flocculent waxy secretions surrounding the eggs coalesce and completely cover the trunks of the infested trees. Long festoons of ghostly white threads hang from every leafless twig and branch. Numerous other trees were also infested to a lesser degree, but the mass infestations on the bucayo trees were most conspicuous. Within a few years, however, such mass infestations were no longer noticeable, and have not since appeared, only rare occurrence on other hosts having recently been identified. As noted in "The Insects of Puerto Rico" (*Jour. Agr. Univ. P. R.* 32(1-4): 1-975, illus., Río Piedras, 1948), "the present scarcity of this scale is due almost entirely to the introduction by Mr. D. L. VanDine of an Australian ladybeetle, *Cryptolaemus montrouzieri* Mulsant, brought into Puerto Rico for the control of mealybugs on sugarcane. In captivity in Puerto Rico they fed upon the sugarcane mealybugs provided, but when released in cane fields, they promptly flew out in search for mealybugs or soft scale insects that were more readily available than those under cane leafsheaths." Admittedly, exposed mealybugs and soft scale insects have not entirely disappeared in Puerto Rico, but in recent years they are exceptionally scarce. Their scarcity constitutes an excellent and typical example of commercial control by a ladybeetle, not too closely specialized in its feeding habits, which continues to be present indefinitely in small numbers.

In much the same way, after the original mass infestations of the cottony cushion scale, *Icerya purchasi* Maskell, on citrus in Puerto Rico had been eliminated by introduced ladybeetles and native parasites, it ceased to have any economic importance.

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A few individuals may at times be noted on casuarinas on wind-swept beaches where *Rodolia cardinalis* (Mulsant) gets blown away, and the entomogenous fungus, *Spicaria javanica* Bally, cannot develop, but any scattered infestations elsewhere only serve to maintain a supply of the ladybeetles.

In sharpest contrast to these ladybeetles that have continued to exist in limited numbers subsequent to the period of initial greatest abundance when their preferred hosts were most numerous, quite different in the story of *Chilocorus cacti* (L.). This large ladybeetle, entirely black except for a conspicuous crimson spot on each elytron, was brought from Cuba in large numbers in June 1938 ((*Rept. Puerto Rico (Federal) Expt. Station for 1938*, pp. 100-102)) and releases made at various points in Puerto Rico. Not only did the beetles disperse widely to all parts of the Island, but they were subsequently found in Hispaniola, and on Mona Island were observed eliminating *Pseudoparlatoria ostreata* Cockerell on wild papayas and *Aspidiotus destructor* Signoret on coconuts in April 1944. A line of the gregarious larvae moves like a tidal wave on a mass of scale insects, leaving not a single living individual in its wake. Local control is total. So common had the beetles become, and especially so useful in eliminating infestations of *Pseudalacaspis pentagona* (Targioni) on cultivated papayas, that no one realized that they had already eaten up all acceptable food in Puerto Rico. The last individuals noted in Puerto Rico were devouring these scales on mulberry at Río Piedras, December 3d, 1943. Since there were no longer infestations of *P. pentagona* and *P. ostreata* on papaya, it seemed to make no difference that there were no ladybeetles to feed on them. At that time nobody gave a thought that possibly the scales might eventually come back. Indeed, it was not until nearly twelve years later, on September 27, 1955, that a heavy infestation of *P. pentagona* was observed on a previously unrecorded host: young trees of "almendrón", *Prunus occidentalis* Sw., high in the mountains near Doña Juana, in the Toro Negro Unit of the Forest Reserve.

*C. cacti* also absolutely cleaned up infestations of *Asterolecanium pustulans* (Cockerell), first recorded from Puerto Rico by Mr. August Busck in 1900. For the next forty years, the pustules or rings of hypertrophied plant tissue growing up like miniature volcanic craters around the scale were almost invariably present on oleander, terribly deforming the tender young shoots and leaves. Not only were mature trees killed, such as those introduced by the local Forest Service because of their rapidity of growth: the Australian silver oak, *Grevillea robusta* Cunn., and *Cassia siamea* Lam., but attack on the endemic tree maga, *Montezuma speciosissima* Sessé et Moc., became serious in 1940-41. The adherent dead, dry leaves of entire lower branches were most conspicuous on roadside magas, seeming to threaten the destruction of this most valuable tree. The last infestation of *A. pustulans* noted in Puerto Rico was September 2, 1941, on *Colubrina ferruginos* Brongn., at Guánica, being eaten up by adults of *C. cacti*. The first observed re-appearance of this scale was on oleander at Río Piedras, March 7th, 1956, or fourteen and a half years later. During this interval, despite intensive search at times for a scale which is most conspicuous because of its type of characteristic injury, not one instance of infestation by the pustule scale was noted. That two such formerly omnipresent scale insects—most favored for attack by *C. cacti*—should re-appear after an absence of twelve to fourteen years, coinciding with the disappearance of the ladybeetle for the same period, is one instance of too perfect biological control. It is, of course, too early yet to know whether *C. cacti* did survive somewhere on the Island, or whether all individuals starved to death: surely a sad result of their thoroughness and effectiveness in eliminating scale insects.

Economically, the losses due to the insidious attack of scale insects on forest trees, or on such specialties as papayas and mulberry, are negligible as compared with those from the endemic white grubs of Puerto Rico. White grubs were formerly not only the major pest of sugarcane, but also of every other crop produced in Puerto Rico. Until 1917 they had not even been named, when E. G. Smyth described the largest coastal species as *Phyllophaga portoricensis*, and its analogue in the western coastal region as *Phyllophaga vandinei*. At that time, effective soil insecticides had not been invented, and biological control by native parasites and predators was largely negligible.

In 1920, a small shipment of the giant Surinam toad, *Bufo marinus* (L.), was received from Barbados and releases made by Mr. D. W. May at the Mayagüez

Experiment Station. In 1923-24, the Director of the Experiment Station at Río Piedras, Mr. R. Menéndez-Ramos, in person brought individuals of the same species from Jamaica. Feeding largely on May beetles, which are the adults of the white grubs, ten years later the descendants of these few toads, having found the coastal environment admirably suited to their needs, had increased to millions. As detailed in "The Rise and Fall of the White Grub in Puerto Rico" (*American Naturalist* 24: 183-193, May-June 1950), they produced a perfect solution of what had formerly seemed an insoluble problem. To be sure, areas of serious white grub infestation could still be found in 1931. By 1932, no such areas were reported from the coastal regions, and no white grubs at all in the cane fields of the South Coast where they had previously been most abundant. Commercially, the problem had been completely and satisfactorily solved. In a desperate search for food, dispersing toads even invaded the mountainous areas, regions too cold for their survival in winter.

The exact status of white grub population can not be observed directly, except when the land is being plowed, and one can judge only by abundance of adults attracted to light, and by remains of beetles in toad excrement pellets. "What the Giant Surinam Toad, *Bufo marinus* (L.), is eating now in Puerto Rico" (*Jour. Agr. Univ. P. R.* 21(1): 79-84, ref. 3. January 1937), showed that in 1935 and 1936 other Scarabaeid beetles to some extent had displaced the economic May beetles as a principal source of food. This was hardly surprising considering how rarely *Phyllophaga* beetles came to light any more. Indeed, considering how little suitable food remained for them to eat, and regardless of their reputed longevity, it was even more surprising that as many toads survived to produce so many excrement pellets for examination.

The rapidly growing algal slime covering submerged vegetation or earth of pools in which the strands of toad eggs are laid furnishes an inexhaustible source of food for the hatching tadpoles, and the little toads on emergence from such pools feed on little terrestrial spiders and mites, on leafhopper and planthopper nymphs and on omnipresent ants. The lack of bulk food for adults is serious, and as a last resort they might be forced to eat caterpillars of *Laphygma frugiperda* (S. & A.), as was observed at Guánica in September 1937. Possibly they can survive on cutworms; but a big juicy cutworm is a snare and a delusion, consisting mostly of ingested plant tissue: chips of cane leaves of little nutritive value for toads. But they can scarcely extract much nourishment from earth, of which the excrement pellets examined towards the last seemed mostly to consist. Yet it was not until 1947 that the question was asked: "What has happened to the Giant Surinam Toad, *Bufo marinus* (L.), in Puerto Rico?" (*Revista de Agricultura de P. R.* 38(1): 25-29, Fig. 7. January-April 1947), because no toads were available to control small incipient infestations of white grubs that had recently begun to appear. The answer: after making due allowance for predators and other factors, complete disappearance almost entirely due to starvation in the immediately preceding years.

The "ultimate check" on toads, due to total (or almost total) extinction of May beetles: their principal source of food, came in the years after 1937 and continued possibly for less than ten years, although commercial elimination of white grubs had already occurred five years earlier. Such a parallelism between the extent of time during which certain scale insects and predaceous ladybeetles disappeared from Puerto Rico may be merely a coincidence. It seems worthy of record, however, as indicating what actually happened in an insular environment in two cases of altogether too perfect biological control by an introduced predator.





# Review of Biological Control of Insect Pests in Japan

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In Japan attempts at biological control have been made against the following insect pests:—

## COTTONY-CUSHION SCALE, *Icerya purchasi* Maskell

This pest was first discovered at Okitsu, Shizuoka Prefecture in 1911, when it was already infesting an area of several acres. In the same year the so-called vedalia, *Rodolia cardinalis* (Mulsant), was received from Formosa, into which island it had been introduced from California and Hawaii in 1909 with great success against the scale. The control of this pest in Japan was successful, as in many other countries.

## SPINY BLACK FLY, *Aleurocanthus spiniferus* (Quaintance)

In 1922 the black fly was first discovered at citrus orchards in Nagasaki Prefecture, Kyushu. It probably had been introduced from South China several years previously. Subsequently it spread rapidly and became a serious pest of citrus plantations in many sections of Kyushu. In 1925 Professor Silvestri, who at that time visited the Orient to search for natural enemies of the red scale, *Aonidiella aurantii* (Maskell), in behalf of the State of California, discovered *Prospaltella smithi* Silvestri, a promising parasite of the black fly, in South China. This parasite species was immediately introduced into Japan. After mass-rearing at the Nagasaki Agricultural Experiment Station, colonies were liberated in several districts. Soon after the liberation the pest became difficult to find. This is one of the splendidly successful examples of the biological control of insect pests.

## RUBY SCALE, *Ceroplastes rubens* (Maskell)

The ruby scale is one of the most destructive pests of various plants, especially orange, tea and Japanese persimmon in the southern part of Japan. It was probably introduced into Japan more than forty years ago. The introduction of parasitic Hymenoptera against the scale was attempted in 1924, when *Scutellista cyanea* Motschulsky was introduced from California, and during the years 1932-1938, when *Aneristus ceroplastae* Howard, *Microterys kotinskyi* (Fullaway), *Tomocera californica* Howard, and *S. cyanea* were introduced from California and Hawaii. However, these parasites have failed to become established.

Professor Yasumatsu discovered in 1946 that promising native parasite, *Anicetus beneficus* Ishii et Yasumatsu, at Fukuoka in northern Kyushu. Liberations and colonizations of the parasite into areas where it is non-existent were first made in 1948 and these attempts have met with apparent success everywhere. This is an example of the successful utilization of a native parasite for biological control purposes. A paper presenting details of this work will be read by Professor Yasumatsu at the present section.

## YANONE SCALE, *Unaspis yanonensis* (Kuw.)

The yanone scale was first found at Nagasaki about fifty years ago and has since spread throughout the southern half of Japan, and is a very destructive pest of citrus. In 1955 *Aphytis lingnanensis* Comp. was imported from California and became established, but its effectiveness in control has not yet been demonstrated.

## MEALY BUGS, *Pseudococcus* spp. et al.

In 1931 the lady-bird beetle, *Cryptolaemus montrouzieri* Mulsant, was introduced into Japan from Hawaii to prey upon mealy bugs. It was propagated at the Okayama Agricultural Experiment Station and liberated in the field. However, it has proved to be not as successful as the vedalia against the cottony-cushion scale, for the climatic conditions in Japan appear to be unsuitable in some respects for maximum effectiveness of this beetle.

WOOLLY APPLE APHID, *Eriosoma lanigerum* (Hausman)

This pest was probably introduced into Japan from the United States on imported apple seedlings more than ninety years ago. The promising parasite, *Aphelinus mali* (Haldeman), after the failure of two consignments in 1925 and 1926, was finally received alive from Oregon in 1931, and became established and successful against the aphid, as had previously occurred in many other countries. Recently, however, outbreaks of this pest have occurred in several localities. As in other countries, this situation may be the result of use of DDT, BHC, parathion and other new insecticides for control of various other apple insects, as these insecticides appear to interfere seriously with the activity of *A. mali*.

ASIATIC RICE BORER, *Chilo suppressalis* (Walker) = *Chilo simplex* (Butler)

The rice borer is one of the most serious pests of rice in Japan. In 1928 the larval parasite, *Spathius fuscipennis* Ashmead, was brought from the Philippine Islands, but establishment failed because winter conditions in Japan are adverse to the parasite. In the following year the egg parasite, *Trichogramma chilonis* Ishii, was introduced from the Philippine Islands. However, as this species has proved to be indigenous to Japan also, the introduction was ineffectual. The mass-rearing of *T. japonicus* Ashm. and *T. chilonis*, by utilizing the eggs of the almond moth, *Ephestia cautella* Walker, and their field liberation to control the rice borer, were first conducted in 1929 at the Shizuoka Agricultural Experiment Station. The experiment was continued for about ten years, but the results were not as satisfactory as we hoped.

ORIENTAL FRUIT MOTH, *Grapholitha molesta* (Busck)

This pest is an endemic species of Japan. In 1923 three promising American parasites, *Macrocentrus ancylivorus* Rohwer, *Glypta rufiscutellaris* Cresson, and *Pristomerus ocellatus* Cushman, were introduced from New Jersey and liberated in several localities. However, these parasites have not been recovered.

RICE LEAF BEETLE, *Lema oryzae* Kuwayama

This beetle is one of the serious pests of rice in the cooler regions of Japan. In 1929, a test was made to determine the value of releases of the native egg parasite, *Anaphes nipponicus* Kuwayama, into rice fields where it was non-existent and the outcome was successful, but this practice has not yet been undertaken on a large scale.

BEAN WEEVILS, *Bruchus rufimanus* Boheman, et al.

In 1930 the egg parasite, *Uscana semifumipennis* Girault, was introduced from Hawaii into Japan for control of *Bruchus rufimanus* Boheman, *B. pisorum* (Linné) and *Callosobruchus chinensis* (Linné). The breeding of this parasite was successful in the laboratory, but establishment in the field has failed.

WHITE GRUBS AND CATERPILLARS OF FOREST INSECT PESTS

The utilization of bacteria and fungi for the control of white grubs (*Anomala rufocuprea* Motschulsky, et al.) and caterpillars (*Dendrolimus spectabilis* (Butler), *Liparis fumida* (Butler, et al.) has been studied by pathologists and entomologists of the forest experiment stations since 1925. Some recent experiments have indicated the possible use of fungi belonging to the genus *Spicaria* in combating the white grubs, but these investigations are still in the experimental stage.

In conclusion, although only a few attempts in biological control have been made in Japan, some outstanding successes have been attained. There are many other serious insect pests, e.g. the vegetable weevil, *Listroderes costirostris* Schoenherr, the potato tuberworm, *Gnorimoschema operculella* (Zeller), and the fall webworm, *Hyphantria cunea* (Drury), to which the biological method could well be applied, and biological control activities are becoming more and more promising in Japan.

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### DISCUSSION

HARVEY L. SWEETMAN. Have *Cryptolaemus* beetles, whether reared and liberated seasonally, failed, as well as those developed under field conditions?

C. WATANABE. Some tests were conducted under outdoor conditions in a small scale in order to establish the predator, but it became apparent that the beetle in question could not withstand the severe winter conditions in Japan.





# El Control biológico de los Insectos agrícolas en el Perú

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Lima, Perú

## ABSTRACT

The biological control of insects of agricultural importance is well developed in Perú. Beginning in 1904, the white scale of cotton, *Pinnaspis minor*, was controlled by importations of different beneficial insects from U.S.A., Barbados, Italy and Japan. In fruitculture the woolly apple aphid is controlled by *Aphelinus mali*, the citrus cottony cushion scale by *Rodolia cardinalis*, and the black scale, *Saissetia oleae*, by *Aphycus lounsburyi*, *Lecaniobius utilis*, and *Scutellista cyanea*, all beneficial insects imported from the U.S.A. The introduction of *Cryptolaemus* and *Ascogaster* did not give good results, and the Argentine parasites of the fruit fly *Anastrepha* failed too. The transfer of *Hippodamia convergens* from California to Perú was very successful. In sugar cane the borer, *Diatraea saccharalis*, was not controlled by *Lixophaga* and *Metagonistylum*, but the native fly, *Paratheresia claripalpis*, is now artificially multiplied and gives a very good and economical control of the borer. In cotton, the eggs and first instar larvae of *Heliothis virescens* are easily destroyed by predaceous bugs of the families *Anthocoridae* and *Miridae*, reared in corn plants specially planted in the cotton fields. The same corn plants give a perfect biological control of *Argyrotaenia sphaleropa*, noxious for cotton, acting as a trap plant and supporting the respective parasites and predators.

Un resumen de las diferentes labores ejecutadas en el Perú para combatir insectos dañinos por el "método biológico" he dado en el año 1939 al Sexto Congreso Científico de la Zona del Pacífico, en San Francisco (Wille 1941). Desde esta época, hasta hoy día, estas labores han aumentado considerablemente en magnitud y en importancia económica. En el Perú cuando en alguna zona apareció una plaga insectil, la que se suponía poder combatirla por el método biológico, se han importado del exterior los predadores o parásitos, o se ha usado los propios enemigos del País, incrementándolos o transplantándolos internamente.

Históricamente, la primera labor del control biológico fué ejecutada en los años 1904 á 1912 contra el piojo blanco del algodón *Pinnaspis minor* (Townsend 1912). Para combatir esta grave plaga que azotó el algodón en la zona de Piura y Chira, se realizaron numerosas importaciones de parásitos y predadores del piojo blanco, trayéndolos desde Barbados, Estados Unidos de Norte América, Italia y Japón y además se propagó los enemigos naturales del piojo encontrados en otras zonas del Perú, trasladándolos desde la región de Lima a la de Piura. En esta obra han contribuido en forma muy útil para controlar el piojo blanco, los siguientes insectos: *Aspidiotiphagus citrinus*, *Arrhenophagus chionaspidis*, *Microweisia* (*Scymnus*) sp. y varios otros como varias especies de *Prospaltella*, varias especies de *Aphelinus*, etc. Por esta labor, que fué acompañada por trabajos culturales, cambiando la forma de cultivo del algodón, ha sido posible controlar al cabo de pocos años, por lo menos en sentido económico y práctico, la grave plaga del piojo blanco en Piura y en otras regiones del Perú.

Para combatir el conocido pulgón lanígero *Eriosoma lanigerum*, se importó desde los Estados Unidos de Norteamérica el *Aphelinus mali*, en el año 1922 (J. O. Solano (Wille 1952, pg. 293)). Esta importación al principio pareció que no había tenido éxito, pues no se pudo encontrar más tarde los parásitos útiles. Pero, en el año 1930, yo he descubierto de nuevo el *Aphelinus* en varias huertas de Lima y después lo he propagado y distribuido en todas las zonas donde hacía daños el pulgón lanígero. Así, al fin, esta importación del *Aphelinus* ha tenido buen éxito y hoy día este útil parásito está bien establecido en todo el Perú.

En el año 1932 apareció en varias plantaciones cítricas el pulgón blanco *Icerya purchasi*; inmediatamente importé de Estados Unidos de Norte América el escarabajo *Rodolia* (*Novius*) *cardinalis* (Wille 1933); esta importación fué un éxito completo: en cada zona del Perú en que existía la *Icerya*, las *Rodolias* han conjurado por completo

esta plaga. Muy interesante es el hecho que actualmente las *Rodolias* en una zona del País (Huánuco) se han alojado sobre las *Iceryas* que atacan a la planta silvestre retama (*Spartium junceum*) y que así, sin provocar ningún daño, se conservan en un medio natural como en un insectario.

La queresa negra *Saissetia oleae*, en los años antes de 1936 hizo graves estragos en los antiguos olivares del Perú; por eso, en 1936, desde la Estación Experimental de Citricultura de Riverside, California, se importaron las siguientes avispidas útiles: *Scutellista cyanea*, *Aphycus lounsburyi* y *Lecaniobius utilis*. Estas avispidas fueron libertadas en el valle de Yauca, que estaba muy infestado por la *Saissetia* y que proporcionó condiciones muy especiales para este ensayo de control biológico (Wille 1937). La proporción de las avispidas libertadas fué aproximadamente de 100 *Scutellista* por 60 *Aphycus* y 6 *Lecanobius*. La revisión del ensayo, en el mes de Abril de 1937, esto es cuatro meses después de la liberación, demostró que las avispidas se habían aclimatado bien, que se habían propagado y distribuido sobre una vasta extensión de los olivares y que habían controlado bien en estas zonas a la plaga de *Saissetia*. La proporción del número de las avispidas había cambiado en una forma muy característica, pues la distribución proporcional en los olivares era aproximadamente la siguiente: 100 *Lecaniobius* por 10 *Scutellista* y por 3 *Aphycus*. Esta proporción, hasta hoy día, esto es durante veinte años ha quedado casi constante. Las avispidas controlan perfectamente las *Saissetias*, siempre que las condiciones climato-ecológicas sean propicias para ellas: pues exigen un ambiente seco y caluroso. Así entre las *Saissetias* y las avispidas se ha desarrollado una cierta oscilación: en el Invierno, con su alta humedad y baja temperatura, las queresas negras se aumentan mucho y las avispidas bajan en número, pero en el Verano, por su calor y su relativa sequedad, las avispidas aumentan de nuevo, controlando así a las queresas.

Los ejemplos de control biológico hasta ahora mencionados, han sido todos de muy buen éxito. Pero debemos mencionar también aquellos ensayos que han tenido un resultado dudoso o negativo.

En los años 1936 hasta 1938, he probado varias veces la introducción del escarabajo *Cryptolaemus montrouzieri*, para el control de diferentes especies de *Pseudococcus*. Apesar de que mis trabajos fueron muy atentamente ayudados por la División de Introducción de Parásitos (C. P. Clausen) del Bureau de Entomología en Washington, ninguna de las diferentes importaciones del *Cryptolaemus* ha dado un resultado positivo; los escarabajos han muerto al cabo de dos meses y sus larvas nunca han alcanzado su desarrollo definitivo. Los ensayos del *Cryptolaemus*, por esto, debemos considerarlos como un caso negativo.

Para el control biológico de la polilla del manzano, *Carpocapsa pomonella*, en el mes de Noviembre de 1937, he conseguido introducir una colonia de *Ascogaster carpocapsae*. Esta colonia se mantuvo en calefacción y se constiguió alrededor de 100 avispidas adultas que fueron puestas en libertad en una huerta de manzanas cerca de la ciudad de Lima, que se encontró infestada en forma gravísima por la polilla del manzano. No se ha recuperado más tarde ningún ejemplar del *Ascogaster*, de modo que esta introducción ha tenido un resultado completamente negativo.

Una muy grave plaga de la fruticultura peruana es la mosca de la fruta, *Anastrepha fraterculus*; para controlarla, se ensayó en el año 1942 la introducción de los parásitos naturales de esta mosca, que en la Argentina controlan la plaga hasta un cierto grado. Así, en el año 1942, en colaboración con la Estación Experimental Agrícola de Tucumán (República Argentina) se importaron 418,000 pupas de *Anastrepha*, de las cuales se criaron 11,551 parásitos de *Diachasmoides tucumana*, *Diachasmoides anastrephae* y *Eucoila pelleranoi*. La cría artificial de estas avispidas en jaulas no daba resultados, tampoco su masiva liberación en dos huertas cercanas a Lima (Wille 1952, pg. 257). Así esta importación de los parásitos de la mosca de la fruta no era un éxito. Interesante es, que recién, en el año 1955, en una limitada zona del Perú (Huánuco), se ha descubierto un parásito natural de la *Anastrepha*, la Braconidea, *Opius trinidadensis* (Gahm.). Estamos actualmente empeñados en el ensayo de aumentar esta infestación natural por métodos artificiales.

Muy interesante ha quedado el ensayo de importar y aclimatar en el Perú el escarabajo útil *Hippodamia convergens*. En el año 1937 fué implantado desde California



una gran colonia en la Estación Experimental Agrícola de La Molina, para controlar los Áfidos de los árboles cítricos (Emilio Guimoye). Durante tres años no se pudo encontrar de nuevo este insecto, de modo que se creyó que la introducción había sido un fracaso. Pero al final del tercer año, reapareció la *Hippodamia* en unas quebradas altas de los valles de la Costa. Así, siguiendo sus antiguas costumbres de California, las *Hippodamias* habían migrado a las cumbres nevadas altas de los Andes, donde paulatinamente se propagaron y aclimataron. Hoy día, *Hippodamia convergens*, es un insecto común en toda la Costa del Perú, pero abunda en los meses de verano y queda escaso en el invierno, en cuya época migra a la cordillera alta.

Muchos esfuerzos se han hecho en el control biológico del barrenado de la caña de azúcar, *Diatraea saccharalis*. Desde el año 1927, la avispa *Trichogramma minutum*, fué criada artificialmente, según el antiguo método conocido con *Sitotroga cerealella*, en la hacienda azucarera Cartavio en Trujillo (E. Gr. Smyth). Los resultados eran satisfactorios, pero no concluyentes. Lo mismo aconteció con el *Trichogramma*, cuando se crió en haciendas algodoneras contra los huevos de varios insectos algodoneros.

Así, para el control del barrenado, se debía buscar otra solución y se introdujo al Perú la mosca cubana *Lixophaga diatraeae* (L. C. Scaramuzza). Estas implantaciones artificiales, con las respectivas operaciones de inoculaciones artificiales en el laboratorio, comenzaron en gran escala en el año 1951, pero ya dentro de un año se pudo reconocer que la *Lixophaga* no prosperó bien en todas las zonas del País, una vez no favorecida por el clima, y otra vez gravemente impedida en su desarrollo por la competencia con la mosca parasitaria indígena *Paratheresia claripalpis*. También la introducción de la mosca brasileira *Metagonistylum minense* como parásito del barrenado de la caña y su multiplicación artificial en el laboratorio en zonas más cálidas del Perú, no ha dado hasta hoy día resultados positivos. Pero todos estos trabajos para controlar biológicamente el barrenado de la caña han tenido un resultado muy bueno: las moscas parasitarias extranjeras no se han aclimatado bien al Perú, pero la mosca nativa *Paratheresia claripalpis* fué reconocida como un parásito muy eficaz. Se desarrolló una técnica de inoculación y multiplicación de la mosca *Paratheresia*, absolutamente idéntica como la de la *Lixophaga*, con muy buenos resultados, de modo que en el año 1955 con *Paratheresia* se han hecho 271,721 inoculaciones y 191,544 liberaciones de moscas *Paratheresia* adultas en los campos cañaverales (Risco 1955). Por esta labor eficiente del control biológico, la intensidad de infestación de la caña de azúcar en el campo ha bajado de 21.9% en 1954 á 10.5% en 1955, o una reducción de 52.1%, y



comparando la infestación desde 1952 á 1955 la reducción es de 61.3%. Estas reducciones de la infestación de la caña se manifiestan naturalmente en el aumento de producción de azúcar en los ingenios. Usando los cálculos de Martorell y Bangdiwala (1953), quienes determinaron que cada 1% de infestación por el barrenador representa una pérdida de 0,1597 de tonelada de azúcar por fanegada, la reducción en la infestación en los cañaverales del Perú, será igual a una recuperación de 9,7896 toneladas de azúcar por fanegada, realmente un óptimo resultado del control biológico.

Al final de esta exposición resumida sobre el control biológico en el Perú, sea mencionado el uso de este método en el control de los insectos del algodón. Cuando en el año 1946 comenzaron las aplicaciones de los insecticidas orgánicos, se suponía que ahora sería solucionado el problema del control de ciertos insectos que no eran controlables con insecticidas minerales, como *Heliothis virescens*, *Pseudococcus* etc. Pero, lo contrario resultó, estas plagas con la aplicación de los insecticidas orgánicos aumentaron en forma desastrosa, porque el equilibrio biológico fué completamente destruido. Después de varios años de experimentación se ha llegado a una combinación de métodos culturales y biológicos que actúa perfectamente bien. Consiste en sembrar maíz en líneas intercaladas cada 7 á 15 surcos de algodón y plantar el maíz en las socas y resocas en los sitios de fallas. Recomendable es sembrar dos variedades de maíz lado a lado: precoz y tardía, para así garantizar una protección más prolongada del algodón (Simon 1954). En las barbas del maíz, las mariposas de *Heliothis virescens* de la primera generación ponen sus huevos é inmediatamente comienzan a desarrollarse chinches de las familias Miridae y Anthocoridae (*Paratriphleps laeviusculus*, *Rhinacloa carmelitana* etc.) que comen y destruyen los huevos y los primeros estadios de larvas de *Heliothis*, evitando así la infestación del algodón. Cuando el maíz está madurando y el algodón más avanzado, *Heliothis* pone sus huevos en los brotes terminales del algodón. Los chinches predadores migran del maíz al algodón y continúan con su obra benéfica, permaneciendo desde entonces en el algodón. En esta forma se aumenta en el maíz intercalado rápidamente, al comienzo de la temporada, el número de los predadores, y mas tarde continúa el constante control biológico que suprime la plaga de *Heliothis virescens* completamente durante toda la temporada.

Hace tres años apareció en forma de plaga en los algodones de la Costa Central del Perú, provocada por las masivas aplicaciones de insecticidas orgánicos la polilla *Argyrotaenia sphaleropa*; su control por insecticidas era imposible y antieconómico. Pero el Maíz intercalado, plantado por el control de *Heliothis*, funcionó como planta trampa: las hembras de *Argyrotaenia* pusieron sus huevos con frecuencia en las hojas de maíz. Inmediatamente en las plantas del maíz desarrolló un control biológico muy efectivo: las posturas de huevos fueron parasitadas por *Trichogramma* y *Telenomus*, las larvas en el maíz por *Apanteles* nueva especie y *Pimpla* sp. y las pupas por las mismas *Pimpla* y las moscas *Nemorilla angustipennis* (Larvaevoridae). Así, este gran complejo de parásitos disminuyó tanto la plaga de la *Argyrotaenia*, que la plaga únicamente por el control biológico desapareció. Así, se ha demostrado que por el manejo cuidadoso de una planta auxiliar (el maíz), se puede controlar en el algodón dos graves plagas, que por insecticidas no son controlables.

En esta forma resumida, he demostrado, que en el Perú, aparentemente por sus condiciones ecológicas y climatológicas especiales, se puede usar los métodos de control biológico en una forma muy eficaz en el combate de los insectos nocivos a la Agricultura.

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### DISCUSSION

L. C. SCARAMUZZA. Did you mean that now they don't use any organic insecticide on cotton?

J. E. WILLE. The biological control of the cotton insects in Peru is so good that only at the end of the season is it sometimes necessary to use organic insecticides. The same farmers have asked the government to restrict the use of organic insecticides by official order of the Plant Sanitary Service.





# Some Reflections on the Causes of Insect Outbreaks

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## INTRODUCTION

As a practicing entomologist my existence came to an end in 1929 on the termination of the *Levuana* campaign in the Crown Colony of Fiji. Since then I have been successively Director of Agriculture in Uganda, Director of the Agricultural and Forest Services in the Sudan, and Principal of the University College in Khartoum. In these capacities I have been concerned with the organization and encouragement of the scientific services.

With this background I have great diffidence in presuming to present any sort of paper to this particularly august and erudite tribunal. I can certainly say nothing that you do not already know, and all I feel competent to do is to refer to outbreaks of insects with which, in one way or another, I happen to have been concerned; to attempt to assess the main causes; and to point to the ever-increasing need to study environment as an essential preliminary to devising methods of prevention and control.

## THE COLORADO POTATO BEETLE, *LEPTINOTARSA DECEMLINEATA* SAY

I will take the initial plunge with this familiar example of a farm crop pest because the essential facts are particularly simple. I used to see this insect, with its power to decimate a crop, in the enormous acreages of potatoes in the Mount Katahdian part of the State of Maine, and in the contiguous Aroostook County of New Brunswick.

Three hundred years ago all this superb potato land was under mixed primeval forest, and there would not have been room anywhere for a potato plant. In that environment the conditions for an outbreak of the potato beetle did not exist. The conditions for an outbreak have been contrived wholly by the industry of man who has replaced that old forest with a fine piece of open, rolling, agricultural country ideally suited for the culture of the Andean potato.

As if to promote the welfare of the ten-lined beetle, we annually grow in pure stands, extending over many miles of country, its favourite food. Deep snows afford protection for its hibernation. We have, in fact, so changed the environment as to create ideal conditions for the development of outbreaks.

In its original home in the Andes the host plant occurs sparingly amongst many others, and for lack of concentrated areas of food is of no economic importance, being in a condition of reasonable balance.

The massing of food supplies, such as the Andean potato, so as to create ideal conditions for insect outbreaks is, of course, a commonplace in agriculture, particularly where mixed farming cannot be practiced. Dozens of examples will come to mind to all of us, varying in detail according to where we happen to have spent our lives: the greenhouse full of tomato plants; a terraced hillside in Italy or Greece devoted entirely to grapes; the Gezira scheme in the Sudan with its two hundred thousand acres of cotton; and so on.

In all such cases we have inevitably created ideal conditions for insects living originally innocuously to become major pests.

## THE COFFEE BUGS OF UGANDA, *ANTESTIA LINEATICOLLIS* STAL. AND *A. FACETA* GERM.

These are major pests of Arabian coffee in Uganda, were difficult to control, and have done a vast amount of damage.

Control was, however, eventually brought about as a result of the observation that they had the power to mount an outbreak only when the food plant was growing on an acid soil. In Toro, where the soils are strongly acid, the coffee estates have now gone over to tea which is doing extremely well. Estates with soils on the border line, of say pH 6, are coping with the bugs by the adoption of cultural practices designed to make

the soils more nearly neutral or slightly alkaline. At elevations below about 4500 feet *Coffea robusta*, which is immune to *Antestia*, has largely replaced *C. arabica* on the more acid soils. In the Bugishu hills, where Africans grow a two thousand ton crop on basic soils, the trees have remained practically immune from *Antestia* attack.

There is no accounting for tastes. We do not know, for instance, why these bugs feed on the tender berries of Arabian, but not on other kinds of coffee; or why it likes the juices only of its favourite food plant when it is growing on a slightly alkaline soil. I have introduced *Antestia*, however, as it seems to be a particularly good example of a first-class pest having been reduced to impotence by changing its environment in such a way as to make the juices on which it feeds distasteful by growing the host plants on a particular sort of soil.

### TROPICAL DESERT LOCUSTS

While plagues of locusts, which we now know to have been either the red, the desert, or the hairy chested, have been known from Biblical times, yet, the outbreaks now seem to be more severe and frequent than formerly. If this is so, it leads inevitably to that useful little word 'why'?

In Saudi Arabia, and in the Sudan, the breeding grounds are part of those vast camel, sheep and goat-grazing grounds of the Bedouin Tribes, where the rainfall lies somewhere between four and six inches per annum.

Such a rainfall does not support the growing of crops but does support the growth of Acacias and other scrubby bushes, and a growth of grasses that becomes denser on the ground and richer in species as one gets further from the four-inch isohyet.

In these Arab countries, even at the back of the beyond, the competition for grazing lands is very keen. On the very edge, for instance, of the great Rub el Khali, or Empty Quarter, in Arabia, the ground is covered with camel dung, and the bushes of the two species of *Acacia* that occur are both dwarfed and gnarled and have all the appearance of having been grazed very hard for a long term of years.

It seems probable that this very hard grazing, particularly by goats, has considerably altered the composition of the flora by reducing the proportion of bushes and increasing the open expanses. In the Sudan, for instance, Dr. John Smith has shown that when bits of this sort of land are fenced against grazing for a few years, a notable increase of bushes takes place.

Another human activity achieving a similar result, but on a smaller scale, is the cutting of desert scrub for fuel. At the town of Abha, for instance, in Saudi Arabia, there now exists a fringe of land extending out for ten to fifteen miles that has been denuded of bushes from this cause.

As desert locusts lay their eggs in open grassland, it seems probable, therefore, that both egg-laying sites and food for the hoppers have been vastly increased since the Arab invasion of the Middle East and Africa by the wood-cutters and by Bedouin grazing.

If this interpretation of the known facts is correct, then the locust outbreaks have assumed their present severity and frequency as a result of mankind having changed the desert environment so as to make them possible.

Once the locusts have become migratory one would not expect parasites or insect predators to have much practical importance in control, and studies made by many investigators has confirmed that this is so. It may not be so generally appreciated, however, that social birds, including Abdim's, the white and the Marabou storks, and the common kite, make a habit of attending locust swarms and that when the swarms are reasonably small, the birds sometimes do great execution. Also, small outbreaks of hoppers have been known to have been eliminated by the depredations of birds of various kinds. Birds are, therefore, probably of very considerable value in lengthening the intervals between outbreaks.

It would, of course, be quixotic to attempt to make locust-proof the millions of square miles of Bedouin grazing lands throughout Africa and the Middle East. Fortunately, this is not necessary. The brilliant work done by Dr. B. P. Uvarov and other locust investigators has shown that the great migrations of locusts, which breed

as they travel, all have their origin in a few comparatively small, permanent breeding grounds. It is in these permanent areas that there would seem to be at least a possibility of so changing the environment once again so as to make it unsuitable for locusts, and so bring about a permanent and natural control.

I have lived nearly twenty years in Africa and can claim at least a rudimentary knowledge of the Bedouin way of life. I know that immense political and other difficulties would have to be faced and overcome before such changes could be made, even in these comparatively small, but still very substantial, areas. It seems inevitable, however, that with the food pressure against mankind daily increasing, a permanent control of locusts will fall to be devised in due course in these permanent foci of outbreaks.

#### THE LEVUANA MOTH OF FIJI, *LEVUANA IRRIDESCENS* B.B.

The coconut palm has a seed that remains viable, when afloat in the sea, and its natural habitat is along the seashore, starting inland from where a seed happens to have been thrown ashore, perhaps during a storm, and certainly at the top of a spring tide. Being tolerant of salt spray, the palm easily takes possession of well-drained areas of flat land along the seaboard, and it occurs naturally as pure stands, sometimes as small forests, in these situations.

The planting of estates to the coconut has increased the numbers of the palm to a small extent but it remains a very small element of the Fijian forest. This is not, therefore, an example of an outbreak occurring on a host plant growing in an environment transformed by man, but rather of one occurring on a host plant reasonably in balance with the flora as a whole.

The control is an old story that was written up many years ago, but for the purposes of this paper, I will repeat the few essentials.

On the main island of Viti Levu the coconut never thrived as the trees were incessantly defoliated by the larvae of *Levuana*. This had been happening for at least ninety years because tree trunks of the oldest specimens showed the characteristic constrictions, due to defoliation, down to the base.

Shortly before 1924, the moth was somehow carried, presumably by wind or ship, to the Island of Levuka and its small outliers. On these islands the palms had always done well and were the main source of revenue and their decimation by *Levuana* caused the gravest anxiety. If it could travel so far, then why not to Vanua Levu and the many other copra-producing islands?

The absence of insect parasites on Viti Levu seemed to indicate that it was not indigenous and that it had probably been accidentally carried there by ship or storm from a nearby island in the South Pacific.

With this assumption to work on Ronald Paine, T. H. C. Taylor and I solemnly set out to search the vastness of the South Pacific area from Fiji to Malaya hoping to find either the original home of *Levuana*, where it might have been a comparatively rare insect, or parasites of a related insect feeding in the same manner and likely to attack the purple moth.

The answer to our prayer was the tachinid fly, *Bessa remota* Aldr., feeding in Malaya and Java on the related *Artona catoxantha* Hmps. n.

The fly was taken to Fiji and within the space of three years reduced the status of the *Levuana* moth to that of a somewhat rare insect.

In the cases of the examples previously discussed the root cause of the outbreaks has been a man-made modification of the environment of the host plant to favour the insect. In this case the outbreak was caused by a change in the environment of the insect itself by its flying across an ocean barrier and leaving its major parasite behind.

This is biological control in the narrow sense. In the rather special cases in which it can be applied it is, of course, the best and cheapest of all methods of control, but opportunities for its application were ever infrequent and rare, perhaps, becoming fewer. In the last three decades a great work has been done over the world in redistributing parasites and predators that have been left behind after the emigration

of their hosts. In this work L. O. Howard, Harry Smith, W. R. Thompson and A. B. Baird have played a major part.

### THE FALL WEBWORM, *HYPHANTRIA TEXTOR* HARR.

On returning to Canada in 1912 after three exciting seasons at the Gipsy Moth Laboratory at Melrose Highlands, Mass., I was encouraged by Dr. Hewitt to begin a long-term study into the causes of insect outbreaks. It was a time when severe outbreaks of such things as grasshoppers, army cutworms, the forest tent and spruce budworm were all too frequent and when the causes were but dimly understood.

After very careful consideration, the comparatively innocuous fall webworm was chosen as a main feature for this study. It, or a near relative, likely to have similar controlling factors, extended from coast to coast; it was easy to locate, even when scarce; it was known to increase and decrease in waves; its natural food plants were the two riverain alders. Although it fed on apple, which had been increased by human industry, yet the original environment of the main food plants had been little disturbed and was not so greatly different from what it probably was, say three hundred years earlier. It was, in fact, ideal for the purpose.

After seven years, the results were duly published as a Canadian Government bulletin, and in this article the briefest reference to the broad results will suffice.

Outbreaks on the potato beetle model did not develop because the food supply did not occur in solid stands over great areas.

Within the limits imposed by food supply, however, the *Hyphantria* population varied with presence or absence of a fairly effective sequence of insect parasites. At the close of one of these waves of increase, when the webs became thinly scattered, insectivorous birds, in particular a species of vireo, became the main factor in control and could, and sometimes did, wipe out the webworm over large areas.

When moths on the wing were again blown into one of these areas of near extermination, they would leave their parasites behind and it sometimes took the parasites several years to build up to useful numbers.

In British Columbia there was a fairly useful tachinid parasite, *Lydella hyphantriae* Tothill, that did not occur east of the Rocky Mountain barrier. As most tachinids probably came into existence with the oak and the ash and the alder in Lower Cretaceous times, it seems probable that this particular one has, from time to time, ranged over the whole of Canada and that it became left behind the mountain barrier after a temporary eclipse of *H. textor* on the eastern side.

The net result of the study was to show that in the case of this example of an insect living under conditions not greatly disturbed by *Homo sapiens* and very similar to its original and natural environment, there was an effective natural control resulting from distribution of food supply, the presence of a sequence of parasites, and the presence of important insectivorous birds.

Control was not the object of the study as in Canada the insect was of little economic importance. Had it been desirable, however, to reduce the height of the waves of increase, it would have been sensible to move the western tachinid across the Rockies and to arrange near orchards little woodsy places designed as nesting places for vireos.

*Hyphantria* has since crossed the Atlantic and become established in Europe. Its control there may prove much more difficult because the original *Alnus incana* ecological zone has been largely destroyed. There is, however, a clear case for introducing the sequence of North American parasites, and for arranging near orchards specially prepared nesting places for any local insectivorous birds that may be found to feed upon the larvae.

### THE GIPSY MOTH, *LIPARIS DISPAR* L.

I naturally select this standard example of an imported insect assuming epidemic proportions in its new environment as I had the inspiring privilege of working for three seasons at the Gipsy Moth Laboratory of the United States Bureau of Entomology under Fiske and C. H. T. Townsend, on the life-histories of the tachinid parasites.



At that time, 1909-1912, a few things were clear. The insect was of major importance and doing a great deal of damage in Massachusetts and New Hampshire; the outbreaks were of annual occurrence, and something had to be done to control them. The parasites had been left behind in Europe and it was common sense to liberate them in America, screened of their secondaries. This work was duly carried out at the behest of L. O. Howard, who, for so many years adorned the United States Bureau of Entomology as its distinguished chief.

Looking back on the problems after some forty-five years, it is easier to see it in perspective as many facets have become clearer.

In the infested area the preferred food of this insect proved, in the main, to be one or other of the several species of oak indigenous to the region, and these trees occurred in pure and nearly pure stands over very considerable areas.

Such a concentration of oaks, and a few other species liked by the larvae, is probably quite unnatural as the primaeval forest was almost certainly much more mixed with nothing like such a high proportion of these trees.

In the face of this concentration of preferred foods, arranged by the ingenuity and perseverance of the human race, it seems improbable that the European parasites will in themselves bring about a stabilization of the gipsy moth at the level of an innocuous member of the fauna. It seems unlikely that the required balance can be achieved until the ingenuity of man applies itself successfully to changing the environment once again so as to remove the concentrations of the preferred trees and replacing with mixtures containing a goodly proportion of species distasteful to the gipsy moth. With the food supply in reasonable balance, the parasites now established would probably come to exercise a major role on the model of those of *Hyphantria*.

#### THE TENT CATERPILLAR, *MALACASOMA DISSTRIA* HBN.

This insect was studied by A. B. Baird and myself as a second string to our *Hyphantria* bow.

I can still vividly remember being one day in the New Brunswick woods in a pure stand of poplar. There was a rain of fraas that made a continual patter and the trees were being completely defoliated. Sitting on a log we wondered what had gone wrong with nature's series of controls to enable this insect to develop such an outbreak. I have been wondering ever since but the problem is clearer today than it was in the wonderment of that baptismal rain.

After some years' study, it was found that the parasites were unable to prevent outbreaks; that starvation due to defoliation usually marked the end of an outbreak; and that the starvation was often accompanied by a flacherie type of disease. This disease, as in the case of a similar one on the gipsy moth, came into the picture only after, or in the course of, a major outbreak and had no influence in the prevention of new outbreaks.

It became clear eventually that the outbreaks were due to the development of pure stands of poplar resulting from a combination of cutting operations and forest fires.

In the primaeval forest of New Brunswick, some isolated examples of which occurred at the time of our studies, there were no pure stands of either of the two indigenous species of poplar, and they occurred only as individual trees or in small clumps. Under such conditions the scarcity and isolation of the preferred food plants would have made outbreaks impossible and the sequence of parasites would have played an important role in reducing the height of the minor waves of increase.

In orchards the apple concentration is usually insufficient to enable an outbreak to develop, and, if it does, it is promptly dealt with mechanically. No orchard is, however, immune to sudden attack so long as clouds of moths from pure stands of poplar in the forest are liable to drift in all directions over farming lands.

#### THE WHITE PINE WEEVIL, *PISSODES STROBI* (PECK)

It is now almost impossible to grow white pine commercially in the Maritime Provinces because the grub of this curculionid beetle feeds upon and destroys the

leading shoot so that, although young growth of the pine is abundant on suitable land, yet the young trees become gnarled and misshapen and of no commercial use.

In contrast with the present position is the fact that in the ancient forest *Pinus strobus* L. was a splendid tree. It was one of the first forest products to be utilized and for many years, until the supply was exhausted, a flourishing industry was based upon it.

Cutting operations, plus forest fires, have, of course, completely altered the environment of both beetle and food plant.

In the ancient forest, white pines occurred as single specimens or little clumps in a mixed, closed-canopy, forest a hundred feet or so high. Seedlings could take root only in little openings caused by the death of an ancient monarch, and into which a shaft of light could penetrate. It seems a fair deduction that although *Pissodes* was in those days a member of the forest fauna, it either disliked the lack of light at the foot of these shafts, or was unable to find the young pines growing in such situations. What is certain is that they were, under those conditions, unable to attack in strength sufficient to cause commercial damage.

By contrast the young seedlings of today, in secondary growth, are fully exposed to flying beetles, which drift over the forest at seedling level, instead of a hundred feet or so above it; they are exposed to full light and every pine seedling is vulnerable to attack.

This, then, is just another case in which outbreaks have been caused or made possible by man himself, who has altered out of all recognition the environment in which the food of the insect is grown.

### THE SPRUCE BUDWORM *CHORISTONEURA FUMIFERANA* (CLEM.)

In the decade preceeding 1924, when I transferred to Fiji to look at the *Levuana* problem, a severe outbreak of this insect occurred in New Brunswick and my last work in Canada was largely devoted to attempting to ascertain the cause.

Cores taken from the largest trees shewed that there had been several periods of restricted growth of spruce trees in the preceding 120 years and that the further one went back in time the less severe and the shorter in duration they became. These periods of restriction were not due to climate because tree species not attacked by budworm did not shew them. It seems a fair assumption that most, if not all, of them had been caused by the feeding of *C. fumiferana* larvae.

The ancient forest must be presumed, therefore, to have been incapable of supporting an outbreak of this insect. Why?

Although this insect is called the spruce budworm, it shews a marked preference for the balsam fir, *Abies balsamea* (L.) Mill., and this fact seems to be the key to the causal problem.

One had only to go into one of the remaining fragments of the ancient soft-wood forests of New Brunswick to realize that the balsam fir was, prior to the coming of civilization, a very minor and occasional ingredient.

Forest utilization, coupled with forest fires, has almost eliminated this ancient and balanced forest and there has arisen in its place a regeneration that is entirely different.

In the ancient forest, when a spruce tree died of old age, its place would be taken by a suppressed seedling, already perhaps one hundred years old, activated into growth by the release of ground space and a shaft of light through a hole in the canopy. Balsam could not have established in such situations because its seedlings need full light for their establishment and growth. It seems fairly certain that balsam occurred chiefly as a fringing species springing up on land freed from forest by the action of rivers and by unusual winds of hurricane force resulting in swaths of forest being blown down.

Letting in the light by clean-cutting and from forest fires has greatly favoured balsam regeneration vis à vis spruce, and we now have vast areas of almost pure stands of the preferred food plant of the budworm.

Under these conditions of massed food supply, as in the cases of the gipsy moth, the tent caterpillar, and the potato beetle, insect parasites and insectivorous birds together become incapable of preventing or controlling outbreaks, and all they can be expected to do is to lengthen the periods between outbreaks.

Once again, therefore, *Homo sapiens* is the chief culprit by so changing the environment as to make conditions ideal for the outbreak of an insect that was in prehistoric days in a state of balance and somewhat rare.

It seems to follow that control of this insect is a matter of applying the ingenuity of entomologists, foresters, ecologists, commercial interests and all those directly concerned, to the end that the forest environment will again be changed so as to eliminate the vast pure stands of the preferred food plant of this pest.

### FINAL REFLECTIONS

If, in this entomological ramble, I have correctly interpreted the known facts, it is a sobering thought that all the outbreaks of potato beetle, coffee bug, desert locust, gipsy moth, tent caterpillar, white pine weevil, and spruce budworm are primarily due to changes made in the environment resulting from the ever-restless activities of man in utilizing the gifts of nature for the needs of an ever-mounting population.

It is true that the insects able to achieve outbreaks are at this stage of civilization so few, as compared with the total number of insect species, as to correspond only to a few grains on a beach of sand.

It is also true, that by changing the face of the earth, the human race is constantly adding to this list of dangerous or highly injurious insects. Europe, for instance, has reached the stage in which manual reforestation is being practiced on an ever increasing scale with great areas being planted to a single species. Unless we proceed with the greatest care, we may find that we have created perfect conditions for yet other insect species, of no economic importance in a balanced forest, to become pests of first-class importance in the new environment we are fashioning.

It gives one to think that the relatively few insects now able to stage outbreaks cause an immense amount of economic loss, and often great hardships to the human race. If we think for a moment only of the human food and forage destroyed by the tropical desert and other locusts, of the industry wiped out by the white pine weevil, and of the ravages caused by the spruce budworm, the total damage is enough to stagger the imagination.

By way of conclusion I venture to suggest that while we have the clear duty to control, as best we may, outbreaks of injurious insects of all kinds, yet the time has come at least for some of them, to set our sights toward prevention rather than control.

The natural control of the spruce budworm, of the white pine weevil, or of any one of the tropical locusts, is likely to prove to be a long-term project and difficult to achieve. It is, however, an infinitely better and more satisfying objective than that of destroying mechanically and in perpetuity huge outbreaks over vast areas.

To bring about such a control, or prophylaxis, we need to work with nature and not against her, and we need to give very serious thought indeed to changes in the environment that have made the outbreaks possible. We have changed the environment once; we have it in our power to change it again; and we should now, I suggest, be making long-term plans for doing so. Such an inspiring objective may be difficult to achieve but is well within the compass of modern biological science.



# Principles of Biological Control of Weeds

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## ABSTRACT

*The framework for biological control of weeds and the hesitancy in its use derive from: 1) the conflict in general acceptance of a plant as a weed, coupled with the fact that introduced enemies of weeds recognize no geographic boundaries; and 2) the risks involved as balanced against the probabilities of success.*

*The conflict in interest may depend upon where the plant occurs and in what ways it may be beneficial as well as harmful. Very complicated, contrary interests may be involved. The more simplified the economy of an infested region the less likely are the chances of disturbing conflicts of interest.*

*Biological control of weeds carries with it serious potential dangers; therefore, precautions to avert these dangers are essential. The probability of success should far outweigh the estimated risk. Recent work on the nature of host selection by phytophagous insects may eventually place this phase on a more predictable basis. Meanwhile, extensive testing of host acceptability is the only guarantee against excessive risk. A review of the reported cases of insects which have "changed their diet" lends no disturbing element to prospects in this field.*

*The chance of success must be appraised for each specific case. Undue emphasis has been placed on forms which attack the plants in particular ways. It is highly desirable that the introduced agents, in interaction with competition by other plants, can destroy existing stands. Curtailment of seed production alone in some cases is insufficient. Emphasis has also been placed on use of this method only for introduced weeds, weeds of natural areas, or those of perennial nature. While these are the most promising subjects, there is no reason to exclude other examples from consideration.*

## INTRODUCTION

Weeds are a principal deterrent to more abundant realizations in agriculture. There are vast regions where weeds either do not yield to chemicals applied against them or else this solution is otherwise impracticable. Biological control has been used largely as a last resort, but with eminent success, against some of the world's most pernicious and otherwise unsolvable weed problems.

The objective in this work is simply to reduce a weed to a status of no economic significance. Eradication is contrary to the principles involved. Control may be accomplished by the direct action of the introduced agents or through actions set in motion by them. The important feature is the result obtained, regardless of the pattern of achievement.

Employment of biological control of a weed has been approached reluctantly for two reasons: 1) the risks involved as balanced against the anticipated chances of success; and 2) its questionable, over-all noxiousness, coupled with the fact that phytophagous agents introduced for its control would be free to spread to other areas where the plant may be of value.

The ecological foundation of biological control in general, and the close relationship between biological control of insects and of weeds in particular are obvious. The generally accepted principles which may be assumed to apply in this work will not be discussed at length. Only certain aspects not widely accepted or previously emphasized will receive attention. Also, no attempt will be made to review the currently active programs in this field. A more comprehensive, general paper covering the field of biological control of weeds will appear shortly through another publication source.

Tillyard (1930) and Sweetman (1936) referred to the inverse aspect of biological control of weeds compared with that of insect pests. This should not focus attention away from the fact that the fundamentals are the same. The two fields are inverse only in that in the one case, plants are the pests whereas the control of insect pests



by this means is for the *protection* of plants. Insects have been the predominant agents used in each field.

Williams (1954) stated a questionable "premise" in biological control, "the theory that underlies the biological control of weeds is relatively simple and is applicable only to alien weeds. It postulates that the great increase of reproductive rate and vegetative vigor that a plant may show after its introduction into a new country is due primarily to a lack of natural enemies, implying that in its native country its comparatively innocuous status is maintained by such enemies . . ." There is no complaint with the view that with weeds which reach excessive abundance when introduced into a new country, the reason *may* be due to an absence of natural enemies, and in whatever event, there is greater likelihood of a successful outcome in the introduction of natural enemies to control them, even if their excessive abundance in the new country (compared with the original) is *not* primarily due to an absence of natural enemies in the new home. A natural enemy which is relatively ineffective in an original environment where potentials of abundance are very restricted, for example, may prove very effective in a new environment composed of quite different biotic as well as atmospheric and edaphic attributes, and where the host plant may reach much higher levels of abundance (see also Wilson, 1949). In the new region the host-density threshold for effective action of the natural enemy may be surpassed while in the original home it is not.

Thus, while aggressive and abundant alien pests are good prospects for biological control, it does not follow and is ecologically unsound to postulate that its excessive noxiousness is necessarily due to an absence of the natural enemies which attack it in its native land. There are far too many other reasons why a pest may be relatively innocuous in its native land yet aggressive and troublesome in environments new to them. Wilson (1949) stated that the physical environment of the invaded region where a weed is very noxious is not likely to be "more favorable than that of the indigenous area in conjunction with which the plant has evolved." However, the present author is of the opinion that this would apply only to the perfection of adaptation to the specific physical conditions. The *extent* of the physical conditions most closely conforming to those adaptations could just as well be far greater in the invaded region, and, hence, the weed would have far greater potentials of abundance irrespective of natural enemies.

The native home of a plant (or an animal) does not necessarily present the maximum in favorableness, considering climate, soil, and other plant competitors. The eminent American ecologist, H. A. Gleason, spent much of his life proving untenable the Clementsian concept of unquestioned, superior adaptation of the "climax dominants". The dominants simply are those which among existing flora possess advantage. The presence of other animals may also affect the situation.

The importance of insects in this respect has been clearly demonstrated by the work of Simmonds (1934) on the control of Koster's curse, *Clidemia hirta* D. Don, in Fiji, referred to later. Osborn (1924) in one of the earliest references, emphasized the possible role of insects as dominant influents in plant competition. He stated, "It has not seemed to me that the control of Pamakani in Mexico has been due to any great extent to the insects and diseases that have been noticed. Still, as I have not seen the plant growing when free from attack, I may possibly underestimate the effect of a retarded growth in competition with other plants." He also stated that if introduced into the Hawaiian archipelago for control of Pamakani, ". . . I feel sure that the Pamakani would be very greatly reduced on the ranches", and again, "A rather slight checking of Pamakani [by the insects] might be sufficient to bring this about".

Obviously then, the physical environment, the influence of animals in changing the advantage of plant competitors, or in opening up a habitat, the respective inherent efficiency of the faunal and floral elements in that environment, compared with that of alien elements, as well as the presence or absence of natural enemies which attack a weed directly, may account for its greater or less noxiousness and abundance in an invaded region, compared with the native home.

On the other hand, there is ample evidence supporting the contention that the abundance of an alien weed (or insect pest) may be due to an absence of effective enemies in the new home, rather than to increased favorableness in other respects.

It remains to be emphasized that these factors may also increase the chances of control by the importation of phytophagous enemies, compared with the roles of these enemies in the native lands, just as readily as they may increase the inherent potentials of the weed in the new region, compared with the old.

## KINDS OF INFESTATIONS AND BIOLOGICAL CONTROL

A weed is any plant where it is not wanted. Obviously weeds have no characteristics peculiar to them alone by which we can either establish their general noxiousness or attack them without endangering, to some degree, desirable plants. This fact is very important in the approach to biological control of a weedy species. Thus, each weed problem must be viewed separately and from many aspects. Dodd (1954) pertinently argued that formulae for evaluation must be elastic in practice.

Generally, with physical, chemical, or cultural methods of control, the effect is automatically limited to the terrain to be cleared of the weed, whereas with biological control the agents of destruction are not so limited. It is thus imperative that a proper evaluation be made of the over-all noxious or beneficial attributes of a prospective weed subject.

A plant may be a pest in one area and valuable in another; harmful to one man's interest and beneficial to his neighbor's; or detrimental to one nation and of value to another on the same continental land mass. As Wilson (1949) stated, "... a weed may be equivocally noxious." Also, Miller (1936) emphasized that future values as well as present ones must be considered.

A few specific examples will illustrate the complexity of decisions:

1. Prickly-pear or *Opuntia* spp. and *Cactoblastis*. Regarding control of this weed, originally infesting 60,000,000 acres of land in Australia, Dodd (1940) stated, "The prickly-pear territory has been transformed as though by magic from a wilderness to a scene of prosperous endeavor." There seems to have been general agreement in Australia as to the remarkable value of this program. On the other hand, Fullaway (1954) reported that cattlemen in the territory of Hawaii objected to the introduction of *Cactoblastis* because *Opuntia megacantha* Salm-Dyck is useful there both as a feed and as a source of otherwise unavailable water on some ranges. In North America there is also considerable opposition to such a proposal for similar reasons and also because of considerations regarding soil and wild-life conservation.

2. Noogoora Burr or *Xanthium pungens* (Wallr.). Dodd (1954) and Wilson (1954) present the cases for and against reopening of investigations looking toward biological control of this weed in Australia by the possible introduction from the United States of two cerambycid stem borers, *Mecas saturnina* Lec. and *Nupserha antennata* Gah. In this case, the complexity does not involve a questionable noxiousness, but an evaluation of the risks to be taken and the chances of success. Wilson stated, "Food tests show that these species might well attack Jerusalem artichoke, sunflower, and certain garden composites, but it is argued that this would be a minor matter compared with the control of Noogoora burr. Unfortunately, there is no guarantee, or even likelihood, that these species would control Noogoora burr. Under these circumstances, the Council for Scientific and Industrial Research Organization, Australia, has been unable to recommend the importation of these insects, and it seems unlikely that the States not affected by the weed would approve the introductions." Dodd's counter presentation was lengthy and pertinent. In general, he felt that the evidence indicates that these insects in nature are not pests of cultivated sunflowers, Jerusalem artichoke or garden composites, plants of minor importance in Australia. He argued that there is evidence that they might prove to be effective agents of control in Australia and that the calculated risk of their introduction would be fully justified if further investigations fail to establish a greater risk than is indicated by the evidence now available.

3. Yellowstar thistle, *Centaurea solstitialis* L. The status of this weed in California, U.S.A., involves the interests of cattlemen, beekeepers, and fruit and seed crop growers. The damage caused by the weed is to the grazing ranges and to fields of small grains. The thistle is said to be important to the maintenance of the bee industry at a level which would satisfy the requirements of bees for the pollination of the very important fruit and seed crops in the State — thus both the beekeepers' and the fruit growers' interests would appear to run counter to the proposal of biological control.

A weed's growth habits, its origin, and the type of land it infests are important to the chances of success. Perkins and Swezey (1924), Tillyard (1929, 1930), Smith (1947), Williams (1954), and others have inferred that biological control is usually not attempted except in cases of urgency, for responsible officials take prior recourse to other methods of control if practicable, because of the risk in introducing phytophagous insects. Land most suitable to this approach is that which is either inaccessible, too low in value for use of other methods, or on which weeds occur which do not yield to other methods. Much progress is currently being made, because of past successes and the greater clarification of the basis of host-plant selection of phytophagous species (e.g., Dethier, 1947), toward wearing down this reluctance to engage in biological control.

Most examples of biological control of weeds have involved alien weeds of perennial habit infesting uncultivated, and usually seminatural range lands. It should not be assumed that only such weeds may be controlled by this means. Currie and Garthside (1932) and Williams (1954) considered that the theory of biological control is applicable only to alien weeds. While the prickly pears, *Opuntia stricta* Haw. and *O. inermis* (D.C.) (consider some synonymous) are lien to Australia, being native to southern North America, *Cactoblastis* was obtained from Argentina and it is not present in the natural home of *O. stricta* and *O. inermis* (Dodd, 1940). If it were introduced there, this moth could conceivably do just as well against these species in the United States where they are native.

An example of the control by a natural enemy of a native plant is that of the removal of the native American chestnut, *Castanea dentata* (Borkh.), by the accidentally introduced fungus, *Endothia parasitica* (Murr.). And. & And. In this case the plant attacked is a very beneficial species, but it is seen that a native plant (or weed) may be even more readily controlled than an alien form. It is thus obvious that natural enemies which attack close relatives of a given weed, native or alien, are potential agents of control.

Regarding weeds of cultivated lands, while row-crop or cultivation practices would interfere with life-history phenomena, the continuity of pressure and success of introduced agents, as contrasted to the case of weeds of undisturbed areas, there is no reason to assume that potential agents for introduction would be incapable of adjusting to such practices and thus incapable of causing marked damage to the weed. Such is certainly the case with many alien insects which attack our crop plants! It is, of course, true that weeds of cultivated crops are more readily controlled by conventional methods, and the economics of such control is more favorable.

The preceding argument is also applicable, with modifications, to the view that perennial weeds are the only promising subjects for biological control. It appears that the answer lies only in the proving with each example.

#### KINDS OF ENEMIES AND THE NATURE OF THEIR ATTACK

Arthropods other than insects and certain vertebrates as well as fungi, bacteria, and viruses are potential agents for biological control of weeds. But, it is likely that the insects will continue to occupy the position of predominance.

Insects may destroy existing stands of a weed by direct action, either strikingly obvious as with the case of *Cactoblastis* and prickly pear or by subtle action and delayed death such as occurs with attack of St. John's wort by *Agrilus hyperici* (Creutz.), with climatic interaction involved (Holloway and Huffaker, 1953). An insect may also destroy a weed indirectly through: 1) cancelling of the competitive advantage possessed by the weed; and 2) the creation of courts of infection for

primary plant pathogens or forms which, although secondarily pathogenic, hasten destruction. An example of the former is the control of *Clidemia hirta* D. Don in Fiji by *Liothrips urichi* Karny (Simmonds, 1934), and to some extent the control of black sage, *Cordia macrostachya* (Jacq.) R. & S. by *Schematiza cordiae* Barb. in Mauritius (Williams, 1951).

Much has been said in favor of insects which attack seeds or which bore in roots or stems. Although safety has been the main reasons for the emphasis (Imms, 1930, 1937; Wilson, 1943), those authors have also expressed the view that these forms are more efficient. It has not been demonstrated that they are better risks or, indeed, any more efficient. There is no valid basis for generalizing. Too few examples among each group have been tried and there are too many subtle ways by which leaf- or shoot-feeders, for example, may accomplish control. The rating of seed-attacking forms as more efficient is quite open to doubt.

The important feature is that whatever the nature of the injury, a really good agent is one which is capable of destroying existing stands of the weed. It is interesting that Wilson later (1949) stated, "It is questionable if insects attacking seeds or fruits of perennials are *normally* very suitable insects for introduction, for the host persists unaffected and the control by seed reduction is likely to prove a slow process, especially as vegetative reproduction is not uncommon in weeds and some flowering is likely to occur in periods when the insects are not active." The long length of viability of some seeds which are missed is also a pertinent point, as is emphasized by Chater (1931).

### RISKS INVOLVED

In the biological control of weeds the serious risks demand precautions to assure adequate safety. As Williams (1954) stated, all other considerations are secondary to whether or not an insect is safe to introduce. There can be no guarantee against risk. There is only the concept of a reasonable calculated risk. The risks are related to the degree of host specificity and the botanical position or special characteristics of the weed. Tillyard (1930) emphasized that the real risk is due to our ignorance of the nature of host specificity rather than to the method itself. The work of Dethier (1947), Thorpe (1939), Thorsteinson (1953), and others is clarifying the nature of host selection, such being based upon the presence of certain chemical and surface features. Yet, it is unlikely that this approach will in the near future replace the practice of determining by trial the host propensities of each insect or natural enemy considered.

To some extent, even the "starvation test" approach fails to answer the crucial question of whether a given insect is capable of seriously attacking plants of economic importance in the particular natural environment where its use is planned. There are probably thousands of phytophagous insects which would, if rigidly tested in the laboratory, feed and perhaps develop upon economic plants but which are never pests of those plants in nature. The evidence from "starvation tests" should be weighed independently in each instance. Dodd (1954) summarized several points of importance:

- "(a) The importance of the weed, and the difficulty of its control by any method other than the biological;
- (b) the potential value of the insect for the control of the weed;
- (c) the value of the economic plant which may be attacked by the insect, weighed against the damage and loss of production caused by the weed;
- (d) the seriousness or otherwise of the damage that might be caused to the economic plant by the insect's attack;
- (e) the simplicity or otherwise of the insect's control by cultural, chemical or other means, if and when it attacked some particular economic plant."

Obviously, the simpler the agricultural economy of a given land mass the less complex the decisions to be made and the lesser the risk to some one of many interests.

Perkins and Swezey (1924), Imms (1930, 1937), Tillyard (1930), Essig (1948), and others referred to many instances of "remarkable" changes in diet of phytophagous insects. Dethier (1947) expressed the opinion that most of these cases represent reversions to an ancestral habit rather than a genetic change. Williams (1954) logically



stated that there is no greater chance that a genetic change will occur in an introduced species making it a threat to some economic plant, than that such will occur among our thousands of presently innocuous plant feeders. Authorities are agreed that with proper precautions, the entomologist is running a permissible risk in introducing insects to control certain weeds.

Also, a review of the instances of "changes in diet" cited by the aforementioned authors makes it clear that these involve oligophagous or polyphagous species. Lists of their host plants have simply become broader with greater knowledge. The examples cited were previously known to attack representatives of several widely separated plant families or genera, and, consequently, their acceptance of still other food plants should have occasioned no great surprise. (Huffaker, 1957).

Aside from the chemical and physical characteristics, an insect may be prevented from attacking a plant if it is not in phenological synchronization with it, or if an intimate hormone relationship is essential.

Wilson (1943) presented a summary of ways of reducing the risks, which will not be repeated here. Huffaker (1957) summarized the considerations involved, the procedures to be used and aspects of interpreting results of tests designed to reduce the risks in introducing phytophagous insects for weed control.

It is obviously imperative that the vast majority of the testing work should be done in the country of origin. Supplemental tests conducted in the country of introduction should be considered only as an *additional* precaution, not as a replacement of the foreign testing.

### CHANCES OF SUCCESS AND THE ROLE OF INSECTS IN PLANT ECOLOGY

In this section, the role of insects in the composition and abundance of plant life is emphasized as a potent argument for the employment of insects and other phytogenous organisms in the biological control of weeds.

Plant ecologists have been slow to investigate this field. Practical entomologists seeking to control weeds by use of phytophagous insects have pioneered here. Wilson (1949) presented the most stimulating account of some of the evidence and Huffaker and Holloway (1949) emphasized certain examples. Ecologists have given much consideration to the influence of man, the larger herbivores, and rodents, on vegetation, by the use of exclosures or arbitrarily protected areas. Almost no attempts have been made to establish insect exclosures for similar purposes, even though many perhaps far more important, highly selective grazers among the insects are abundant on those same ranges. Present-day, selective insecticides and acaricides should be thoroughly investigated as a means of setting up chemical exclosures against certain phytophagous arthropods.

The evidence is of two types: 1) examples of significant action of natural enemies on natural vegetation; and 2) examples resulting from the introduction of agents into new lands for the control of weeds.

EVIDENCE FROM STUDIES IN NATIVE HABITATS: To summarize much pertinent information relative to natural vegetation, there may be mentioned Koebele's studies of insects of *Lantana camara* L. in Mexico (Koebele, 1924); Phillip's (1931, 1935) studies in Cape Province, South Africa, of the role of insects in the "keeping of a proper balance in the organic scale" (climax vegetation); the removal of the chestnut tree, *Castanea dentata* Borkh., from the deciduous forest climax of eastern United States by the accidental introduction of the fungus, *Endothia parasitica* (Murr.) And. & And.; Bew's (1920) conclusion that seed-destroying insects can change the local dominants of a climax forest type without any change in climate; Cook's (1942) conclusions as to the controlling action of the moth *Melitara dentata* (Grote) and other insects over the abundance of cacti in the Central Plains in Kansas, U.S.A., except during years of drought; Wilson's (1943) findings that phytophagous insects in Europe, within the limits set by environment, control the densities of St. John's wort, *Hypericum perforatum* L.; and the very recent studies of Pringle (1955) on the extensive destruction of native Big Sagebrush, by a chrysomelid, *Trirhabda pilosa*



Blake, which suddenly appeared in very destructive numbers on the range near Kamloops, British Columbia, Canada. T. R. Gardner (correspondence with J. K. Holloway) has stated that this has been a recurring situation but that its natural enemies have usually very quickly brought the chrysomelid under control.

EVIDENCE FROM PRACTICAL EXAMPLES OF BIOLOGICAL CONTROL: Regarding the evidence from practical programs, H. S. Smith, the eminent authority on biological control, in personal conversation, has stated that it may be expected that a greater proportional success will result in the employment of biological control of weeds than has been experienced with the use of this method of controlling insect pests. Also, A. P. Dodd (1954), the noted authority on biological control of prickly pear, *Opuntia* spp., in Australia, stated, "... there have been few, if any, failures where a serious attempt has been made to exploit biological control" (in the control of weeds). It is indeed encouraging that in many instances, not one, but several of the introduced insects have demonstrated capacities to reduce stands of their weed hosts. Also, in a number of instances reduction has resulted even though the evidence obtained from studying the insects' influences on their hosts in the native lands was not encouraging.

Some of the reasons for the proportionately good results in this field are: 1) weed subjects have been almost exclusively pests of relatively undisturbed, uncropped range lands where human interferences are at a minimum; 2) such weeds are also engaged in a more intense and direct competition with other claimants of the requisites, many of which become competitively superior at the site as a result of only slight destruction of the weed by a phytophagous insect, without actual death of individuals being occasioned by the insect's feeding; 3) action of insects introduced to control a weed may occasion additional damage associated with encouragement of fungous, bacterial, or other injurious organisms (Dodd, 1940; Wilson, 1943); 4) with weeds, in contrast to insect pests, there seems to be no marked, general deterrent to effective control by introduced agents in temperate regions compared with tropical; 5) attempts made in this field have necessarily been restricted to examples which offer definite promise of success, whereas this has not often been so with respect to introductions for control of insect pests; and 6) there is also introduced a new factor not at all similar to the situation with insect pests. Plants do not usually die from the attack of a single insect, and the net result could be an advantage in greater potentials in locating isolated hosts.

The instances where introduced insects have brought under control an alien weed which had become excessively abundant and aggressive in a new land does not mean necessarily that the weed's excessive abundance in the new home, as contrasted with its status in its native land, was due mainly to the absence there of the insect or insects which were introduced. Effective control in its native home cannot be assumed in the absence of other evidence. If the natural enemies of such an introduced insect are excluded, it may have greater effect over the weed in the invaded region than in its original home, where its own enemies may hold it in check. This does mean obviously that the introduction was a success, and that in the new environment, the insect is limiting for the weed, whether or not this was true in the region native to them.

Examples which may be considered outstanding as evidence are the control of prickly pear, *Opuntia stricta* Haw. and *O. inermis* (D.C.), in Australia by the phycitid moth, *Cactoblastis cactorum* (Berg), introduced from South America (Dodd, 1940); the control of Koster's curse, *Clidemia hirta* D. Don, in Fiji by the introduction of the thrips, *Liothrips urichi* Karny, from Trinidad (Simmonds, 1934); and the recent control of St. John's wort, *Hypericum perforatum* L., in western United States (Holloway and Huffaker, in preparation) by the introduction of the European chrysomellid, *Chrysomela gemellata* (Rossi). Biologists associated with the work of these introduced insects credit to the pressure exerted by them gross general changes in the vegetative cover. In each case much of the land was seminatural and used for grazing.

As somewhat less striking, or as yet, undetermined final result, there may be mentioned: the programs of biological control of *Lantana* in Hawaii by the introduction from Mexico of eight species of insects (see Perkins and Swezey, 1924); the control of St. John's wort, *Hypericum perforatum* L., in Australia and Canada by introduction of *Chrysomela* spp., and a root-boring buprestid, *Agilus hyperici* (Creutz.)

(Wilson, 1943; Parsons, 1954; Smith, in press); the control of black sage in Mauritius by the introduction from Trinidad of the galerucid, *Schematiza cordiae* Barb., and, to a lesser degree, the seed-infesting chalcid, *Eurytoma* sp. nr. *howardi* (D.T.) (Williams, 1951); the program in New Zealand for control of ragwort, *Senecio jacobaeae* L., by the ragwort seed-fly, *Pegohylemia jacobaeae* Hardy; of gorse, *Ulex europaeus* L., by the seed-weevil, *Apion ulicis* Forst., and of piri-piri or *Acaena* by the saw-fly, *Antholcus varinervis* (Spin.) (Miller, 1947); the control of pame-kani, *Eupatorium glandulosum* H.B.K., on the islands Oahu and Maui (Hawaiian Islands) by the introduction from Mexico of the trypetid, *Procecidochares utilis* Stone (Fullaway, unpublished report); and, among others, the various examples throughout the world of control of prickly pear, *Opuntia* spp., by the cochineal, *Dactylopius opuntiae* Ckll. and *Cactoblastis cactorum* (Berg) (Petty, 1948).

### RELATION OF CLIMATE TO THE CHOICE OF AGENTS

Wilson (1949) presented a pertinent analysis of the relation of climate in the selection of species for introduction. Some of his conclusions are:

"1. It is evident that different, but closely-related species commonly play precisely the same role in relationship to the host [plant] in different areas [where the plant has a wider distribution than any of its phytophagous enemies] and that the essential differences between the species consist in their special adaptations to particular climates.

"2. The climates of the regions of distribution of the weed in the invaded and in the native regions should be thoroughly studied as a basis of selection of subjects for introduction.

"3. The insect to be selected should be the species most numerous [rather, most effective] in the region climatically most resembling the climate of the invaded region; and conversely, superiority of an insect in an area dissimilar in climate to the invaded region, is no indication that it will prove of value [or, it can be added, that a form inferior to it there may not prove of more value].

"4. When the phytophagous species becomes so numerous in local areas in the native region as to nearly eliminate the weed, and only one or two species survive in large numbers, these are the important ones. Since it is just such conditions of host-plant control, with resultant severe insect competition that it is hoped to produce in countries where the weed has been introduced, it seems logical to introduce only those species that become dominant in the homoclimate under conditions of local control of the host." This would improve the extreme slowness of such investigations and decrease the risk, if any, in introducing additional, perhaps, unnecessary species.

However, the present author would point to what has become almost a maxim in biological control: that it is extremely problematical to attempt to predict the outcome, or to select in advance the best species for introduction, if based upon climatic analyses alone, although such approaches are to be recommended and should in some cases prove fruitful. Dodd (1940, p. 23) has illustrated this point. If the most promising species prove unsuccessful, other species should then be tried. One difficulty is that of deciding just what are the criteria in equating climates. A small, rather subtle difference in two otherwise very similar climates may be the factor of importance.

In conclusion, the approach of the researcher in this field must be imaginative and flexible, yet very cautious.

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## DISCUSSION

STANLEY E. FLANDERS. The fact that the intentionally-introduced phytophagous insect is brought in without its natural enemies is an important factor in the enhanced chances for the biological control of weeds as compared with the biological control of insect pests, the natural enemies of entomophagous insects being much more generalized and adaptive in their attack.

C. B. HUFFAKER. The general advantage of elimination of the natural enemies, when the introduction is made, was mentioned, but your point that the natural enemies of entomophagous insects are more generalized and adaptive may be a significant point, which was omitted.

P. W. OMAN. Essentially, the question involves the points: Are the risks involved in biological control of weeds greater than in other phases of biological control; and, are the returns, when success is attained, proportionately greater? In brief, is biological control of weeds a good gamble?

C. B. HUFFAKER. Yes, as you are aware, the danger relative to the possibility of an introduced species attacking economic crops is far greater than that involving attack by an introduced species of some beneficial insect. The returns in several outstanding examples have been very substantial. Authorities are agreed that in spite of the risks the method is a very good gamble, if proper precautions are taken.

ALVAH PETERSON. What is the status of the attempt to control wild blackberry plants in Australia or New Zealand?

C. B. HUFFAKER. So far as I know, they are not actively engaged in this work at the present.



# Biological Control of Pamakani, *Eupatorium adenophorum*, in Hawaii by a Tephritid Gall Fly, *Procecidochares utilis*.

## I. The Life History of the Fly and its Effectiveness in the Control of the Weed<sup>1</sup>

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### ABSTRACT

*Eupatorium adenophorum* Spreng., known as pamakani in Hawaii, is a tropical America plant which was introduced into Hawaii about 1860. Following its introduction it thrived and spread, forming dense thickets up to 10 feet tall on valuable grazing lands. Prior to 1945 labor and funds were commonly used to reclaim infested ranch land through the mechanical removal of this weed. In 1945 a tephritid stem gall fly, *Procecidochares utilis* Stone, was introduced from Mexico and within a few years it brought about effective control of the pest on several thousand acres of the more valuable rangeland in certain areas. In other areas, notably on the wet steep slopes on the windward side of East Maui, pamakani plants have been less affected by the fly.

Observations and studies begun in 1949 revealed that parasites of this tephritid gall fly were extremely abundant in certain areas. Five species of parasites were reared and even though parasitization often exceeded 50 percent in the drier areas, parasites have not prevented the gall fly from bringing about effective control of the weed in these areas.

In 1945 a tephritid gall fly, *Procecidochares utilis* Stone (Tephritidae: Diptera), was introduced into Hawaii from Mexico to combat *Eupatorium adenophorum* Spreng. (Compositae), at that time a serious weed pest of rangeland in some areas in Hawaii. The fly increased rapidly under Hawaiian conditions and soon many plants which had been heavily and persistently attacked were weakened and died. The progress of the fly in the destruction of *E. adenophorum* in Hawaii has been followed, and some of the pertinent information obtained on the biology of the fly, its effects on the plant, and the benefits derived from it are presented in this paper.

### GENERAL CHARACTERISTICS AND GROWTH HABITS OF PAMAKANI

*E. adenophorum* is a perennial shrub that grows rapidly, producing many shoots and branches, thus forming dense shade which often crowds out desirable vegetation. This plant, locally known as pamakani, meaning "windblown", produces numerous clusters of the white flowers, and the tufted seeds are widely disseminated by wind. Due to the profuse seed production as well as propagation from stems, which commonly take root when they come in contact with the soil, this plant became widespread and in certain areas extensive acreages of pure, dense stands of pamakani as high as 10 feet developed.

### DISTRIBUTION OF PAMAKANI

The native home of *E. adenophorum* is Mexico but it is now known to occur in Australia, Hawaii, Indonesia, Jamaica, and the Philippines. This plant was brought to Hawaii and planted as an ornamental at Ulupalakua, Maui, about 1860. Subsequently, it escaped cultivation and became abundant over large acreages in that vicinity. Later, it spread to other parts of the island of Maui and became established on Oahu, Molokai, Lanai, and more recently on Hawaii (Davis, 1953). Even though pamakani is widely distributed on Maui and Oahu its distribution on Lanai, Molokai, and Hawaii is limited. It occurs from sea level to elevations of about 7,000 feet in relatively moist to wet situations; however, it does not occur in all the different vegetation zones (Hosaka & Thistle, 1954).

<sup>1</sup>Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Technical Paper No. 376.



## ECONOMIC IMPORTANCE OF PAMAKANI

In Mexico *E. adenophorum* occurs sparsely and is not considered to be a pest. Nevertheless, it became a serious weed on rangeland in certain areas in Hawaii and Australia. Pamakani also occurs in forested areas, and at one time it was feared that much of the native vegetation in Hawaii would be crowded out by this plant (Neal, 1948).

On the island of Maui pamakani increased enormously in the immediate vicinity of Ulupalakua, invading and taking over thousands of acres of valuable rangeland. As a result, attention was called to the seriousness of it as a noxious weed and it became known as the "Maui pamakani". Many acres became so densely covered with this weed that the land produced no feed and cattle would not penetrate the thickets. A devaluation of the rangeland resulted, and thousands of dollars were spent in combating the weed on infested land prior to the success of the gall fly discussed below.

As far as is known, no serious damage has been caused by pamakani to forest vegetation and it is not a serious pest on cultivated land.

## CONTROL

So much of the more valuable land on the Ulupalakua Ranch became overgrown with pamakani that it became necessary to resort to control measures. Between 1920 and 1945, hundreds of acres of grazing land on the Ulupalakua Ranch were reclaimed from pamakani by the removal of the plants mechanically, and crews also spent considerable time laboriously digging out individual plants in outlying areas. In addition to the ranch crews, truck farmers who were given free use of land for 10 years to clear the land of pamakani reclaimed about 1,500 acres of land. Mechanical removal of pamakani on the ranch was continued on an energetic basis until 1948, but it was expensive, slow, and especially difficult on steep slopes and in gulches. Therefore, when a gall-forming fly was reported on *E. adenophorum* in Mexico in 1944, steps were promptly taken to introduce it into Hawaii and it has proven valuable. This tephritid fly, later described as *Procecidochares utilis* Stone (Stone, 1947), was shipped in numbers to Hawaii in 1945 and subsequently released by entomologists of the Territorial Board of Agriculture and Forestry. Upon release, it immediately became established, increased rapidly, and spread to all pamakani-infested areas. Within two years many plants were heavily galled by the fly and due to the optimism over its eventual success in the control of the weed further mechanical control measures were abandoned by 1948. Since this fly was an outstanding success its biology was investigated and will be discussed.

### LIFE HISTORY AND HABITS OF *P. utilis*

**EGGS:** The whitish, elongate eggs, which are about 0.6 mm. in length, are inserted between the young, paired, folded leaves at the tips of the growing shoots (Fig. 1). As many as 20 eggs have been found between a single pair of leaves from field-collected material. The average obtained from samples taken from the Ulupalakua Ranch in February 1956, was 7 eggs per pair of folded leaves. The incubation period was 3 to 4 days during the summer and 6 to 8 days during the winter in the insectary in Honolulu.

**LARVAE:** On hatching, the tiny larvae migrate downward to the base of the leaves and penetrate the tender meristematic tissues. As the larvae continue to feed and the stems to grow, galls are formed in which the larvae complete their development. Occasionally a larva enters the petiole or midrib of the leaf, where a gall is produced and development is completed. There are three larval instars, all of which are whitish in color. The full-grown larva, which is about 4 mm. in length, cuts a circular channel from the central cavity to the outside of the gall, leaving only the semitransparent epidermis or "window", and then returns to the central cavity to pupate. About 20 days are spent in the larval stage during the summer months.

**PUPAE:** The puparia, which eventually become blackish in color, are formed inside the central cavity, and 2 to 3 weeks later the adults escape by breaking the "windows" at the outer end of the exit channels made by the full-grown larvae.

**ADULTS:** Newly emerged adults crawl onto nearby stems and branches where they remain inactive for about one hour while their wings become expanded and dried.

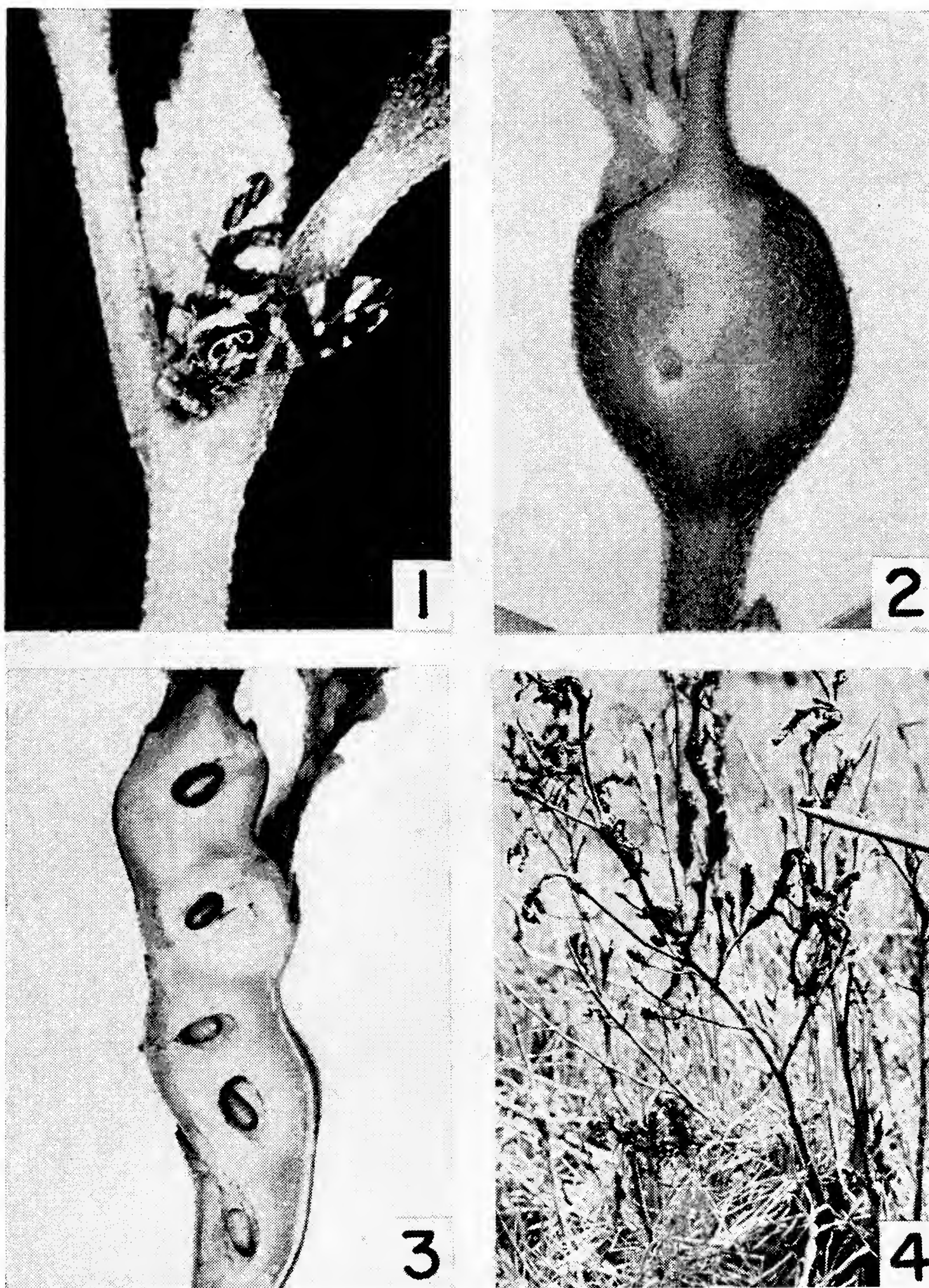


Fig. 1. *P. utilis* female ovipositing between pair of young pamakani leaves. Fig. 2. Simple gall showing window through which adult fly emerges. Fig. 3. Longitudinal section through a compound gall showing puparia *in situ*. Adults had already emerged from lower three puparia. Fig. 4. Heavily galled dead plant. Note the predominance of coalesced galls, indicating persistent attack during elongation of stems.

Mating occurs during the first day and egg laying may also begin the same day. Egg laying continued in the insectary up to 3 weeks; however, the majority of the eggs were laid during the first week. Ten females kept in rearing cages in the insectary during February 1956 laid an average of 171 eggs per female. The average length of life was about 2 weeks and very few lived as long as 3 weeks.

In the field in the Ulupalakua area large numbers of adults of this black and white fly may be commonly seen on pamakani. However, they are more numerous following the rainy season, which is favorable to the development of many succulent shoots



in which the galls are formed and the flies develop. During the drier months when there is relatively little vegetative growth, flies continue to be abundant in this area but are scarcer than at other seasons.

### GALL FORMATION

**DESCRIPTION OF GALL:** The stem where the larva or larvae bore into it begins to show external evidence of gall formation approximately 2 weeks after hatching. As the larva develops, the gall also continues to enlarge, the ultimate size reached about 3 weeks later being dependent to a great extent on the number of larvae present and the vigor of the shoot. Where there is only one larva present, the gall reaches a size of about 15 mm. in length and 10 mm. in diameter on stems that are normally about 5 mm. in diameter. However, when several larvae are present in a simple gall (Fig. 2), it may become as much as 35 mm. in length and 17 mm. in diameter and produce as many as 11 flies. The average number of individuals per gall in a 68 simple-gall sample was 3.0. If egg laying is continuous and the individual stems are repeatedly attacked, compound galls are formed by the younger galls coalescing and becoming a part of the older ones (Figs. 3 and 4). In areas where the fly has been especially effective in controlling pamakani most of the galls are compound ones. One of these composed of 7 coalesced galls measured 175 mm. in length and produced 25 individuals, as evidenced by the emergence holes.

**EFFECTS OF GALLS ON PLANTS:** In the Ulupalakua area where the fly is abundant throughout the year, not only are practically all shoots attacked but they are also attacked a number of times during their growth. Furthermore, oviposition is often so intense that the attacked buds and growing tip dry out and die. In addition to the damage caused by the galls to the physiology of the plant, the emergence holes provide entry for microorganisms that cause decay. The damage to the plant by the fly reduces stem and foliage growth and seed production. During the dry season when there is little vegetative growth with a large fly population present to attack them, the effect of the fly on the vigor and growth of these plants is especially pronounced. Repeated attack causes branches to die and finally reduces the vigor of the plants below the point of survival. However, along the Hana Coast on Maui where the fly population is low and only 10 to 20 percent of the shoots attacked, the fly has caused the death of few or no plants.

### BENEFITS DERIVED FROM THE FLY

Immediately following the release of *P. utilis* in 1945 it increased rapidly, began to reduce the pamakani in certain localities (Bess, 1950; Pemberton, 1951), and subsequently proved to be highly effective in these localities. The most spectacular results occurred in the Ulupalakua area where thousands of acres of land that were once densely covered with pamakani (Fig. 5) have been reclaimed by the activities of the fly and are now highly productive grazing land. Thousands of additional acres are continuing to be reclaimed annually. In fact, all of the known pamakani in Hawaii with the exception of that in the Hana Coast area has been heavily attacked, its vigor reduced, many plants killed, and its spread kept in check. Widely scattered individual plants, as well as dense thickets of pamakani, are heavily galled by this fly. However, destruction of the pamakani on the Ulupalakua Ranch has been noticeably slower on north slopes and in gulches than on other exposures (Fig. 6). Furthermore, there has been little curtailment of pamakani by the fly in the Hana Coast areas, but the areas affected are on steep, wet slopes which are not used for agricultural purposes.

In some places in the Ulupalakua area, grasses, such as Kikuyu, may have had some effect in further reducing the vitality of the pamakani and killing of scattered plants, but in many places pamakani plants heavily galled by the fly have died without competition from grasses, leaving bare soil exposed.

The success of *P. utilis* in controlling pamakani in Hawaii attracted attention in Australia where this plant is also a serious rangeland pest, and an entomologist was delegated to come to Hawaii to make further screening tests on the fly with the hope that it might be safely introduced into Australia. Dodd (1953), who found the fly to be highly specific on *E. adenophorum*, later made several shipments of the fly to Australia.



Fig. 5. Dense stand of pamakani at about 4,000 feet elevation on Ulupalakua Ranch. Photograph taken in 1949 at an early stage in the biological control of the weed. Fig. 6. Intermediate stage in the biological control of a pamakani area on the Ulupalakua Ranch. Foreground was densely covered with pamakani but grasses are coming in as plants die from the persistent attack of the fly. Plants persist longer in gulches and on north slopes. Photograph taken in 1955.

### NATURAL ENEMIES OF THE FLY

Parasites and mice take a heavy toll of the immature stages of the fly within the galls. Five species of hymenopterous parasites [*Opius tryoni* Cameron, *Opius longicaudatus* (Ashmead), *Bracon terryi* (Bridwell), *Eupelmus cushmani* (Crawford), and *Eurytoma tephritidis* Fullaway] have been found to attack *P. utilis* in Hawaii and often parasitization by them exceeds 50 percent. The two opiines parasitize very few *P. utilis*, but each of the other three parasites frequently becomes abundant. Their abundance varies with the seasons, elevation, and perhaps other ecological factors. (This subject will be treated in detail in a forthcoming paper). In making regular



collections of galls in certain localities it has often been difficult to obtain galls that contained larvae and puparia due to the removal of them by mice. Out of 400 galls examined on Mt. Tantalus, Oahu, April 27, 1956, 206 of them had been gnawed into by mice and the larvae and puparia removed. Despite heavy losses caused by both parasites and mice, *P. utilis* has been able to succeed in Hawaii.

### SUMMARY AND CONCLUSIONS

*E. adenophorum*, known as pamakani in Hawaii, is a tropical America plant which was introduced into Hawaii about 1860. Following its introduction for use as an ornamental, it escaped into adjacent areas, spread rapidly, and formed dense thickets up to 10 feet tall on valuable grazing lands. Prior to 1947 labor and funds were commonly used to reclaim infested ranchland through the mechanical removal of this weed. In 1945 a tephritid stem gall fly, *P. utilis*, was introduced from Mexico to combat the weed, and within a decade it has brought about effective control of the pest on many thousands of acres of valuable rangeland in certain areas. Ranchers no longer apply control measures and consider the problem solved. However, in a limited area on the wet, steep slopes on the windward side of East Maui the fly has had little influence on pamakani.

The rapid build-up of *P. utilis* in the Ulupalakua area on Maui, its continued high populations there, and its comparative scarcity in certain other areas, especially along the Hana Coast of East Maui, prompted the study of the progress of the fly and reduction of pamakani. In many areas the fly has been sufficiently abundant to cause many galls per plant during each growing season, which have weakened the plants, and many thousands of them have been killed by the sustained attack of the fly. As the plants in pamakani thickets become weakened and die, those remaining become smaller and more sparse. The fly persists in sufficient numbers to cause heavy galling and stunting of these isolated plants which eventually die, leaving the land completely free of pamakani. This has occurred on thousands of acres of grazing land despite the high parasitization of the fly which has often exceeded 50 percent.

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# Biological Control of *Opuntia megacantha* and *Lantana camara* in Hawaii

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## ABSTRACT

*Opuntia megacantha* Salm-Dyck, a Mexican plant, introduced about 1800, was recognized as a pasture weed about 1930, when on a three hundred thousand acre, improved cattle ranch on the island of Hawaii, it was calculated that about thirty thousand acres were covered with this plant to the exclusion of grass and other forage plants. Opposition on the part of owners of unimproved ranches to the introduction of cactus-feeding insects delayed their introduction until 1948. The first introductions, from Texas and California, proved unsuitable. Later introductions, from Queensland, Australia, where they successfully controlled *O. streptacantha*, proved well adapted to *O. megacantha*, and in the course of five years not only stopped the spread of this tree cactus but destroyed much of the standing older plants so that Guinea and other grasses could be sowed in predominantly cactus areas and the carrying capacity vastly improved.

Encouraged by the success with *pamakani* (*Eupatorium adenophorum* Spreng.) and tree cactus (*O. megacantha*) our attention turned to another American pasture weed *Lantana camara*, which had been the object of investigation more than fifty years previously by Perkins and Koebele, when out of more than a hundred possible enemies of *Lantana* only eight were successfully introduced, due to poor transportation facilities. Reviewing the results of Koebele's work, it was considered possible to obtain and successfully introduce additional and more effective *Lantana* insects than the eight already established. Australia and Fiji cooperating, Mann and Krauss went into the field in 1953 and in the intervening years have collected and shipped to Honolulu for testing three coleopterous, four lepidopterous and one hemipterous insects in sizable lots as well as additional species that either had to be rejected as unsafe or failed to survive. The most promising species are discussed. Only one of these is definitely established, i.e. *Octotoma scabripennis* Guerin. All but one of the remaining six have been propagated and liberated in sizable lots and eventual establishment is confidently expected.

There are many kinds of cactus growing in Hawaii, all of course introduced, at one time or another. However, the only species the ranch owners are concerned with is the tree cactus, *Opuntia megacantha* Salm-Dyck, which was brought in about 1800 — for what purpose I do not know; perhaps there was some thought of developing a cochineal industry. The only useful purpose this plant served, however, was to supply a succulent forage to the poorer ranchers in times of drought. There are two varieties of this species in Hawaii, the red-fruited with weaker spines, and the white-fruited, with larger and stronger spines, and some other recognizable differences.

Our attention was called to the spread of this plant into their best pastures by Mr. A. W. Carter, manager of the three hundred thousand acre Parker Ranch on Hawaii, in 1930, about the time reports were being circulated of the marvellously successful work of the Australian entomologists in controlling their pest cactus with insects secured in America. The Board of Agriculture and Forestry was requested to investigate the possibility of controlling our pest cactus with similar insects. This proposition was being seriously considered by the Board, but on account of the opposition of the ranchers located in the drier sections of the island, who depended on the cactus to carry their herds through times of drought, nothing was done until about 1944 when it was conceded by the ranchers wishing to retain their cactus, that the red-fruited and desirable variety, which could be denuded of its spines, cut and fed to the parched cattle, was slowly disappearing on account of a fungus disease attacking it, and was being supplanted by the white and less desirable variety. Eventually it was agreed that there would be no opposition to the introduction of cactus-feeding insects if the introduction was confined to the island of Hawaii and movement of cactus from Hawaii to any other island would be prohibited.

At first the cactus insects were obtained from California and Texas but these species, with one exception (species of *Chelinidea* which was later rejected), proved unsuited to *O. megacantha*; later three different species developing on a tree cactus, *O. streptacantha*, in Australia, were obtained through the kindness of Alan Dodd of the Brisbane laboratory; these proved suitable to our species of cactus, were propagated, tested as to strictness of feeding-habits in cage confinement with our important economic plants, and eventually liberated on the Parker Ranch, in all sections where cactus prevailed. These species, in the order of their importance, are the lepidopteron, *Cactoblastis cactorum* (Berg.), cochineal, *Dactylopius opuntiae* (Ckll.), and the cerambycid borer, *Lagocheirus funestus*. They were propagated and spread on the ranch, flourished in all sections, and in some sections spread naturally over considerable distances. They have certainly brought cactus under control. Seedling plants are doomed when *Cactoblastis* reaches them. Many older plants succumb to the combined attacks of *Dactylopius*, *Cactoblastis* and fungus. The *Dactylopius* flourishes better in the drier sections and during the summer months; *Cactoblastis* prefers the higher pastures and does better in the winter months. *Dactylopius* suffers from the attacks of coccinellids and other coccid predators; *Cactoblastis* is attacked in the egg stage by *Trichogramma*, in the larval and pupal stages by hymenopterous parasites; the pupae are devoured by field mice. But the populations are only temporarily diminished. The project is generally considered a success.

Whilst the Territorial Board of Agriculture and Forestry of Hawaii has been engaged in biological control for over fifty years, it is only in the past ten that it has put the main effort into biological control of pasture weeds. There are some reasons for this change of objective. First, the two main industries, sugar and pineapple production, have their own experiment stations and take care of their own problems. The cattle industry, which stands to gain by the weed work we are doing, has an association but no experiment station. While it supports the weed work independently and is greatly interested in the results, it looks to the Government to a great extent for technical assistance. The cattle industry also is our third main source of income; it does not suffer from labour troubles like sugar and pineapples; is prosperous and can expand without overproducing. This move into the biological control of weeds gained favor because of striking successes in the control of cactus and pamakani (*Eupatorium adenophorum* Spreng.). The latest work has been mostly on lantana, on which I will now report.

Fiji and Australia are contributing to the lantana and *Eupatorium* investigations, as they are interested in securing better control of these weeds.

Before Mr. Krauss, the Board's explorer, and Mr. Mann, the Queensland entomologist, went into the field in 1953, it was necessary to re-appraise the results of the work done on lantana over fifty years ago. At that time when the disciplines which now prevail in this field of endeavor were unformulated and the transportation facilities which we now have were not even foreseen, of the many insects etc. — hundreds in fact — found by Mr. Koebele in connection with lantana in Mexico and shipped in considerable lots to Dr. Perkins in Honolulu, only eight were successfully introduced and established, and of these eight but three are considered of significant value in reducing lantana. These are the seed fly, *Agromyza lantanae* Froggatt, the tortricid borer in the floral heads, *Epinotia* (*Crociosema*) *lantana*, and the tingitid bug, *Teleonemia scrupulosa* Stal., feeding on the leaves and causing defoliation.

In weed control it is generally considered that considerable progress has been made if a seed-destroying insect can be found, especially if the plant spreads from seed. In Dr. Perkins' view it was the Chinese dove that was spreading lantana, as it was continually feeding on the berries and gradually extending its range. In this it was assisted by the mynah bird, another recent introduction. The spectacular insects, therefore, at that stage were the seed fly and the flower-head borer, and undoubtedly the alarming spread of lantana was arrested. But then, parasites of these insects appeared and consequently their effective work diminished. In many areas lantana continued to flourish. Around 1920 I made an experiment with several thousand seeds collected from damaged flower heads which were planted in flat boxes in our nursery. I was quite pleased when only three or four seedlings came up but continued to water

and care for the planting regularly. After four months, the remaining seed, which had lain dormant all this time, really began to germinate, and I soon had a full stand of seedling plants. But here again, the unexpected happened. When these seedlings had four or five leaves, an infestation of the tingitid bug was noticed, and in less than a week the whole planting was completely destroyed. Perhaps the destruction was so complete because the plants were tender seedlings. Mature plants generally survive. There is also another limitation on the good work of the tingid. It is apparently a lowland, dry region insect, and lantana often grows luxuriantly at considerable elevation — up to two thousand feet, where the annual rainfall may be up to 50 to 60 inches. Dr. Perkins in his work on lantana stressed the necessity of obtaining insects that could accommodate themselves to the higher, wetter country. In Mr. Swezey's survey of the lantana problem, made in the 1920's, he found lantana still very abundant and very much of a pest plant in the Kona section on the island of Hawaii, and I believe this situation is due to climatic differences pertaining to this region. Kona gets a great deal more rain in the summer months than the rest of the island and the farms and ranches are largely in the higher lands around the two thousand foot level. In the lower lands the rains generally terminate around April. By that time lantana is in flush and flowering is profuse. But soon the various insects appear and before long the tingid, which is almost as prolific as an aphid, has so thoroughly covered the foliage and sucked the leaves dry, complete defoliation occurs. Nothing but the bare, dry, woody stems remain. You would believe the plant dead, but when you cut into the stem you find green tissue, and when the fall rains come again, it revives like a desert plant and puts out new foliage. This goes on year after year. Complete defoliation is not enough to kill the plant, apparently. Therefore, the search for additional insects.

Mr. Krauss has spent two years collecting lantana insects, visiting all the countries in Central America and the northern part of South America, Cuba, Puerto Rico, Jamaica and Trinidad, and Mr. Mann spent the better part of a year in Mexico. Scores of different insects found on lantana have been investigated, including some stem-borers, foliage feeders and sucking bugs, also a coleopterous leaf-miner. To date, four lepidopterous insects have been reared, multiplied, tested and approved for release, and are being propagated in our insectary. These are the phalaenids *Diastema tigris* from Panama (also Florida) and *Catabena esula* from southern California, and the pyralids, *Blepharomastix acutangulalis* from Mexico and *Syngamia haemorrhoidalis* from Cuba and Florida; also an additional species of *Teleonemia*, *T. vanduzeei*, has been introduced from Cuba and released; also a chrysomelid beetle, *Octotoma scabripennis*, whose larvae mine the leaves of lantana, the adults puncturing and eating them, has been introduced from Mexico and Honduras, and released. A great deal of attention has been given to two borers, one a cerambycid beetle, *Plagiohammus spinipennis*, the other a hepialid, *Phassus argentiferus*. Stock of the latter dwindled, due to disease, and eventually disappeared. As evidence was obtained later that the species is polyphagous in habit, its further consideration is unlikely. Another cerambycid with a horn-tailed larva and likewise a stem-borer but boring in the terminal twigs rather than in the roots and main stem, *Aerenicopsis championi* has been collected in two different seasons near Vera Cruz (*Plagiohammus* was only obtained in Nogales in the Orizaba region). As difficulty was experienced in its propagation, field releases were made, after the insect had been tested as to host-specificity — specificity of ovipositional instinct — by alternately placing ovipositing females on a lantana plant and on an economic plant of a suitably long list of plants, both in cages and without confinement, from the more than four hundred adults shipped here from Vera Cruz in the spring of 1955. Liberations were made in the Puna district of Hawaii where the environment was believed to be similar to that of Vera Cruz. At the same time the twelve plants that were used in the testing procedure were maintained, and from both these and the Puna plants a generation was reared in the spring of this year (1956), confirming Mr. Krauss's information that the species has but one generation a year, adults appearing from April to June. Collecting was continued in 1956 and over 650 more beetles were sent in and released, some of these being placed in the Kona section of Hawaii, where the lantana usually grows luxuriantly during the summer months. *P. spinipennis* was unobtainable in numbers in 1956 and the prospect of establishing this

species in Hawaii is rather dim, but if it could be obtained again in considerable numbers it would undoubtedly make a valuable addition to the presently established species, as its attack centers on the stem three or four inches above ground, the burrow even extending into the main root. A plant weakened at this part of its structure would hardly survive very long. But there are almost insuperable obstacles to its attainment. As far as we know, never very abundant, it has a long life-cycle, occupying a year or more. The first lots secured were advanced larvae, shipped in cuttings of the stem. In order to bring these to maturity they had frequently to be supplied with fresh wood. Some, however, were reared to adults, were successfully paired, and oviposition secured in potted plants. But here again there was considerable loss of material, as the first stage larvae working in the cambium dried out, due to exhaustion of the spongy tissue in the thin cambium layer. Some testing was accomplished but insufficient to warrant release. And now another season is awaited.



# The Control of *Cordia macrostachya* (Boraginaceae) in Mauritius

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*Cordia macrostachya* (Jacq.) R. and S., a boraginaceous shrub growing to about 15 feet in height, was accidentally introduced into Mauritius at the turn of the last century with cane plants from the West Indies. It spread rapidly over many parts of the island, and became a serious pest of pasture-land and in plantations of Mauritius hemp, *Furcraea gigantea* (Vent.). Eventually it was decided to investigate the possibilities of biological control, and after some preliminary work on the ecology of the plant by Wiehe (1946) and of the insects found on *Cordia* by students at the Imperial College of Tropical Agriculture, full time investigations were undertaken by the Commonwealth Institute of Biological Control. It was decided to concentrate on the most promising single species attacking the plants, study its life-history, alternate food plants and natural enemies in Trinidad, and, if this species appeared suitable, to make shipments to Mauritius for further study and possible eventual liberations. As this study progressed the second most promising species would be similarly investigated in detail. In this way a series of possibly suitable species would become available for release in Mauritius.

The first species investigated were the leaf-eating beetles, *Physonota alutacea* (Boh.) and *Schematiza cordiae* (Barb.). Although defoliating species have not been particularly favoured in the past in the biological control of weeds there seemed no grounds for rejecting them if they proved to be restricted to *Cordia* as a host plant. Both adults and larvae of these species feed on *Cordia* leaves, and the amount of leaf surface consumed per beetle during its life-cycle is considerable. It was shown that heavy defoliation had a very marked effect on growth and seed production of *Cordia* (Callan 1948, Simmonds 1949). Moreover, in the field in Trinidad both species were heavily attacked by parasites, and it was thought that, freed from these, damage caused to *Cordia* in Mauritius would be considerably greater.

Host plant specificity of these two beetles and their larvae was tested in Trinidad (and later in Mauritius), and although starving larvae nibbled and in some cases fed a little on a few plants none was suitable as a host for development of the beetles, and both species were considered suitable for release in Mauritius.

Unfortunately in Trinidad *Physonota* was very restricted in distribution, and this was found to be due to the predacious ant, *Solenopsis geminata* (F.). The ants removed *Physonota* larvae as soon as they hatched from the egg, and hence *Physonota* only occurred in those areas where this ant was absent. On liberating *Physonota* in Mauritius a very similar result was obtained. *Physonota* became temporarily established in one small area only, where ants, excepting *Camponotus* sp., were absent. In other areas *Solenopsis* and *Technomyrmex detorquens* (Walk.) prevented establishment. *Technomyrmex* is not predacious but the young larvae of *Physonota* were disturbed by them and dropped off the bush.

Liberations of *Schematiza* started in Mauritius in March 1948 and initial results were most disappointing, but this was due to the fact that during the dry season (as in Trinidad) adult *Schematiza* are dormant, and no breeding in the field occurred. However in December 1948 at the beginning of the hot, wet season these beetles became active, rapid multiplication occurred, and by March 1949 astronomical numbers of *Schematiza* were present around liberation points, and leaves, flowers and even young bark were stripped from the *Cordia* bushes, which often had 15,000 to 20,000 beetles per bush (Williams 1952).

In the 1950 season many *Cordia* bushes had been killed and *Schematiza* was in general less numerous, owing to lack of food plants, but was still very plentiful and continued to destroy large areas of *Cordia*.

During this time investigations in Trinidad had been transferred to species attacking the inflorescences and seeds. Larvae of several species of Lepidoptera feed on the



buds and flowers of *Cordia* — namely *Chloropteryx* sp., *Racheospila gerularia* (Hbn.) and *R. rufolineata*, *Eupithecia* sp. and five species of Lycaenidae. However, since there is normally considerable natural shedding of flowers and young seeds, it was thought probable that species actually attacking nearly ripe seeds might prove more effective in decreasing actual seed production, and hence preventing regeneration and dispersal of *Cordia* in Mauritius.

There is a complex of minute Hymenoptera associated with full and nearly ripe seeds of *Cordia* in Trinidad. This consists of a phytophagous curytomid, *Eurytoma* sp. near *howardii* D.T., and its parasites, *Eurytoma* sp., *Callimome* sp., *Zatropis* sp., *Pseudochalcura* sp., *Galeopsomopsis* sp., *Tetrastichus* sp. and *Eupelmus cushmani* Cwfd. The last is particularly interesting as it definitely parasitises the phytophagous *Eurytoma* and yet is usually somewhat larger than the host species. The phytophagous *Eurytoma* was studied in both Trinidad and Mauritius, and was finally liberated in 1950 in Mauritius where it spread rapidly — reaching at times some 75% destruction of seeds compared with some 5-10% in Trinidad.

Whilst these investigations were being developed a start was made on the study of species attacking young shoots and also stem borers (no species attacking the roots were found). On young shoots the principal species were the moths, *Lamprosema inabsconsalis* (Mosch.) (Pyraustidae) and *Dichomeris stratella* (Wlshm.) (Gelechiidae), the former being parasitised by *Orgilus* n. sp., *Microgaster* n. sp. and *Macrocentrus* sp., and both by *Apanteles* n. sp. These species could possibly cause considerable damage in prevention of formation of inflorescences. Wood boring larvae of the moth, *Acrodegmia pselaphialis* (Rag.) (Chrysaugidae), were fairly common in old *Cordia* bushes, and in some instances killed branches or even whole plants. Larvae were parasitised by a braconid, *Macronura urichi* (Roh.). However, investigations of these shoots and wood borers were abandoned when it became apparent that *Cordia* was being very successfully controlled in Mauritius by *Schematiza* and *Eurytoma*. Some concern was later felt in Mauritius since the numbers of *Schematiza* dropped considerably. This however was due entirely to the rapid reduction in available food plant as *Cordia* was destroyed. Only a single natural enemy has, to date, attacked these introduced insects in Mauritius — a predacious pentatomid, *Afrius williamsi* (Miller), kills a few *Schematiza* larvae, but has a negligible effect on the populations.

Since 1951 no further liberations have been made in Mauritius. By 1952 large areas of *Cordia* had been killed out, and the most recent information, March 1956, supplied by Mr. J. R. Williams, the entomologist of the Department of Agriculture, Mauritius, states that "Dense *Cordia* growths are now virtually restricted to the southwest of the island, which is an area that was inexplicably never appreciably affected by *Schematiza*. In other parts of the island little *Cordia* is now seen. Vigorous *Cordia* hedges along roadsides which were previously so evident have completely vanished, and some agricultural students now no longer know the plant which was once so familiar to all."

There is, as might be expected, a fluctuating equilibrium between *Cordia* and *Schematiza*, with local increases in *Cordia* being followed by those of *Schematiza*. As Williams points out, if a number of species, rather than just two, were attacking *Cordia* in Mauritius, a more stable equilibrium might be maintained.

*Eurytoma*, Williams says, is everywhere active and must be of great importance, judging by the number of attacked fruits present. Although no recent figures are available as to fruit infestation, it appears to be of equal importance to *Schematiza*, possibly being responsible for the fact that there is no recolonisation of former *Cordia* areas which have been cleared by *Schematiza*.

There has never been any recrudescence of *Cordia* since these introductions apart from local fluctuations, and there has been a general gradual decrease in the amount of *Cordia* present in the last four years.

Williams concludes his comments by saying that no one in Mauritius would contradict the claim that the control had been one hundred per cent successful.

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# The Biological Control of Klamath Weed in California<sup>1</sup>

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## ABSTRACT

In California *Hypericum perforatum* L. is known as Klamath weed because it was first reported, about 1900, in northern California in the vicinity of the Klamath River.

This perennial proved to be very aggressive and in 1944 it had spread to 30 counties and it was estimated that in excess of two million acres of range land had been taken over by this weed.

In most localities the cost of materials and the inaccessibility of the land to be treated had been limiting factors in chemical control.

Biological control by insects had been under consideration for many years as the most desirable approach to this problem but it was not until 1944 that the work was undertaken. This first attempt in North America to control a weed by the use of insects began with the importation and release of *Chrysolina hyperici* (Forst) and *C. gemellata* (Rossi).

In 1950 a root borer, *Agrilus hyperici* Creutzer, a cecidomyiid gall fly, *Zeuxidiplosis giardi* (Kieff), and *Chrysolina varians* (Schall) were imported and released.

All of the imported species became established with the exception of *C. varians*. It was soon evident that under California climatical conditions *C. gemellata* was to be the dominant insect. The rapid clean up and the present degree of control is due almost entirely to this insect. The reproductive phases of the beetle and the growth phases of the plant are in synchronization so that the full reproductive capacity of the insect is realized.

The weed is controlled almost entirely by the larval stages feeding on the winter basal growth. The feeding continues until the late spring after which time rains become less abundant and as a result the plant is unable to sufficiently recover before the dry summer begins.

At the present time, 1956, the weed is under control in all counties and the economic gains resulting from this control has been considerable.

In California *Hypericum perforatum* L. is known as Klamath weed because it was first discovered in the northern part of the state in the vicinity of the Klamath River. This aggressive perennial continued to increase and spread over the state and in 1944 it could be found in 30 counties and it was estimated that in excess of two million acres of range land was infested. The value of heavily infested properties was greatly depreciated, so much so that it was almost impossible for ranchers to borrow money for improvements, and the real estate value was about one-third that of non-infested lands.

The weed was susceptible to most of the weed killers being used in 1944 but large scale control operations were impractical because of the cost of treatment and the inaccessibility of the land to be treated.

Professor Harry S. Smith of the University of California, formerly Chairman of the Department of Biological Control, had been considering biological control of this weed by the use of insects for many years.

The Commonwealth of Australia first began a search for insect enemies of *Hypericum* in 1920, according to a report by Currie & Garthside (1932). Early in 1935, after the British species apparently failed to become established in Australia, the work was transferred to Southern France, the results of which were published by Wilson (1943). The progress of this Australian experiment was watched with interest

<sup>1</sup>This is a cooperative project between the University of California Agricultural Experiment Station and the United States Department of Agriculture, Agricultural Research Service.







in California. In 1944 A. J. Nicholson, in correspondence with Harry S. Smith, reported much progress with the introduced insects. This encouraging report motivated negotiations between the University of California and the United States Department of Agriculture and resulted in the granting of permission to introduce *Chrysolina hyperici* (Forst), *C. gemellata* (Rossi) and *Agrilus hyperici* Cr. This marked the beginning of the first attempt in North America to introduce phytophagous insects to control a weed.

*C. hyperici* was first released in the spring of 1945 and *C. gemellata* in February, 1946. Both species became established, and two years after the first releases there was no further need for importations. Within a very short time it became evident that *C. gemellata* had shown a much greater rate of increase than *C. hyperici*. After three generations it was possible to collect thousands of beetles for redistribution from an original colony of only 5,000 adults, and in 1950 about 3,000,000 adult beetles were collected at this same location.

After about three generations in a locality the beetle larvae become so numerous they completely destroy the procumbent winter basal growth of the plant. This results in an almost complete curtailment of photosynthesis during this critical growth phase of the plant, and as a result the root system becomes weakened and the plant dies.

The detailed life history of *C. gemellata* has been reported by Wilson (1943). The following gross aspects of the life history were reported by Holloway and Huffaker (1951) to show the close relationship of the life cycle of the beetle and the growth phases of the weed under California conditions.

The adult beetles issue during April and early in May from their pupal cells just beneath the soil surface. They feed voraciously on the foliage of the plants, which are producing flower buds or are actually in flower at that time. By the latter part of June and early in July the fully fed beetles seclude themselves beneath stones and debris and in crevices in the soil. When they find a suitable resting place they go into aestivation for the remainder of the summer. The plant also enters a relatively dormant phase, dropping its leaves and becoming dry and woody.

With the advent of the fall rains both the weeds and the beetles become active. The plant forms a leafy, procumbent basal growth, upon which the active beetles feed sparingly. Then the beetles mate and commence egg laying about mid-October. All stages of the beetle (eggs, larvae, pupae, and adults) are able to withstand winter temperatures. By spring most of the eggs have hatched and the larvae are approaching maturity. The third- and fourth-stage larvae feed on the basal growth, which they completely destroy. Early in the spring the plants that have escaped destruction develop upright shoots which are destined to become the flower-bearing stalks. At that time the larvae complete feeding and enter the soil to the depth of about 1 inch, and each forms a cell in which it pupates. This completes the 1-year life cycle of the insect. The perennial plant has also gone through a complete growth cycle.

The success of *C. gemellata*, as contrasted to *C. hyperici*, is due to better synchronization with the climate and the growth phases of the plant. *C. hyperici* reacts much slower to fall rains than does *C. gemellata* and as a result the life history extends further into the spring when the plants become less suitable as food and pupation conditions are less favorable. As a result, the maximum rate of increase is not realized for each generation and this disadvantage has resulted in *C. gemellata* becoming the dominant species.

The root borer, *A. hyperici*, introduced from France,<sup>2</sup> was liberated in 1950 (Holloway & Huffaker 1953). It readily became established and has shown excellent

<sup>2</sup>Dr. H. L. Parker and associates collected and shipped these insects to Albany, California.

← Fig. 1. 1948 — Humboldt County, California — Original release site of *C. gemellata*. Foreground shows viable weed while in the background the plants had been destroyed by the larvae and failed to bloom.

Fig. 2. 1949 — Same field one year later showing complete destruction of the plants and the return of grasses.

ability to destroy dense stands of Klamath weed. *C. gemellata* adults are reluctant to oviposit in shady areas although *A. hyperici* does not make this discrimination and works as well in the shade as in the open. It is anticipated that the root borer will ultimately play an important complementary role in the control of this weed.

A gall fly, *Zeuxidiplosis giardi* (Kieff.) also imported from France,<sup>2</sup> was released in 1950. It also became readily established. The distribution of this insect will be restricted to unusually moist conditions under which the Klamath weed continues to grow during the summer. Such situations are encountered along irrigation ditches or seepage from springs. Because of its environmental limitations it is not anticipated that this insect will be very important in the control of the weed.

A third species of leaf feeding beetles, *Chrysolina varians* Schall., was introduced in 1952.<sup>2</sup> This species failed to become established.

By 1956 Klamath weed has been reduced from the status of an exceedingly important pest of range lands to a casual roadside weed. County appropriations of funds for the control of the weed have been discontinued, and land values have increased with the improved carrying capacity of the ranges. The California State Department of Agriculture has removed Klamath weed from the list of primary noxious weeds in the State. Some twelve years after the first release of the beetles it would seem that the biological control of Klamath weed has been accomplished.

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## DISCUSSION

HENRY A. BESS. Do the beetles require a dense stand to maintain themselves or can they find and destroy isolated plants?

JAMES K. HOLLOWAY. Fortunately no, for isolated infestations have been readily found by adult beetles. One isolated plant 5.8 miles from the nearest large infestation was destroyed.

E. G. ANDERSON. Is any other treatment or management practice needed to effect reclamation of range land (other than release of insects in California)?

JAMES K. HOLLOWAY. Good range management in conjunction with the beetles.

<sup>2</sup>Dr. H. L. Parker and associates collected and shipped these insects to Albany, California.

# Biological Control of Klamath Weed, *Hypericum perforatum* L., in British Columbia<sup>1</sup>

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## ABSTRACT

Populations of the chrysomelids, *Chrysolina hyperici* Forst. and *C. gemellata* (Rossi), first imported into British Columbia from the United States in 1951 as control agents for Klamath weed, *Hypericum perforatum* L., have increased slowly but continuously. Effective control has only begun, however, in one colony of *C. hyperici* at Fruitvale. However, the volume of growth of *H. hypericum* has increased considerably as a result, at least in part, of abnormal production of seedlings because of favourable weather conditions in 1953. The establishment of a buprestid, *Agrilus hyperici* (Cr.), and a cecidomyiid, *Zeuxidiplosis giardi* (Kieff.), imported in 1955, was not determined definitely, and it is believed that the latter species probably perished during the first autumn.

*Hypericum perforatum* L., variously known as Klamath weed, St. Johns-wort, or goatweed, occurs in all but the Prairie Provinces of Canada but is a threat to agriculture only in British Columbia. In the southern interior of this province it has spread rapidly under a wide variety of environmental conditions. Economic losses to date have resulted only from the replacement of useful forage plants and not from dermatitis among livestock. This weed, as in the northwestern United States, is most prevalent in the vast, mountainous, grazing areas in which cultural and chemical control are not practicable.

Two natural enemies, the chrysomelids, *Chrysolina gemellata* (Rossi) and *C. hyperici* Forst., which are satisfactorily controlling the weed in Australia (Wilson, 1950) and the United States (Holloway, 1948) were investigated at the Entomology Laboratory, Belleville, in 1950. Tests of host-plant specificity supplementing those reported by Currie and Garthside (1932) and Holloway (1948) were conducted in quarantine rooms at 72°F. and 60 per cent relative humidity. Canadian species of *Hypericum* tested were: *H. calycinum* L., *H. frondosum* Michx., *H. moserianum* Andre, and *H. olympicum* L., which are grown horticulturally, and *H. boreale* (Britt.) Bickn., *H. spathulatum* (Spach) Steud., *H. kalmianum* L., and *H. perforatum* L. which occur naturally in southern Ontario.

Large colonies of adults of the two chrysomelids from California were liberated in British Columbia in 1951, *C. gemellata* at Christina Lake and Westbank and *C. hyperici* at Fruitvale. Further colonies of *C. gemellata* from Idaho were released at Fife and Edgewood in 1952 and at Waldo in 1954. A large colony of *C. hyperici* from Oregon was released at Edgewood in 1952. In 1956 beetles from the Canadian colony of *C. hyperici* at Fruitvale were released at Waldo and Hardy Mountain (near Grand Forks) and adults of *C. gemellata* from Fife were released at Hardy Mountain. Thus, the two species of *Chrysolina* now occur together at Edgewood, Waldo, and Hardy Mountain.

Cultures of a buprestid, *Agrilus hyperici* (Cr.), and a cecidomyiid, *Zeuxidiplosis giardi* (Kieff.), were obtained in California, where both are well established (Holloway and Huffaker, 1953). These were released in 1955 at Christina Lake in the area where *C. gemellata* was already established.

Populations of *H. perforatum* and of its imported insect enemies were surveyed in six colonies in British Columbia to determine levels at which adequate control of the weed occurred. The change in vigour of the weed that resulted from feeding by the insects was determined by measuring the heights of all the flowering stems in quarter-square-metre quadrats. These quadrats were selected randomly and were permanently marked to permit surveys of the same areas for several years. A grid

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comprised of bronze rods aided in defining the areas and sub-dividing them into 25 parts for ease and accuracy in making the counts. With the grid in position, the proportion of the soil areas occupied by *H. perforatum* and each of the other plant species was estimated to discover the nature of vegetative changes.

Populations of aestivating adults of both species of *Chrysolina* were sampled by removing shallow soil areas of 200 square centimetres with the aid of a rectangular cutter constructed from portions of a large crosscut saw. A soil sample was taken adjacent to each large quadrat, to avoid disturbance of plants for future surveys. Only adults were retained after the soil had passed through a screen sieve of three mesh per centimetre.

Eggs of *C. gemellata* and *C. hyperici* were sampled during early autumn by removing the weed growth from soil areas of 200 square centimetres adjacent to the corners of the large quadrats; samples were removed from a different corner each year.

Larvae of each instar were counted *in situ* because they mingled with the soil particles when attempts were made to remove soil samples. As with the adult survey, samples of larval populations were taken from soil areas of 200 square centimetres adjacent to the adult sampling sites of the previous summer.

Techniques used for sampling and separation of pupae from the soil were identical to those used for the surveys of adults.

The seasonal development of *C. gemellata* under conditions that prevailed at Christina Lake was determined by semi-weekly counts of each metamorphic stage occurring on or beneath ten crowns of *H. perforatum*.

As possible mortality factors were studied briefly. The prey of the single, known colony of the *Formica rufa* group at Christina Lake was intercepted while being carried to the nest by the workers during four-hour periods. The numbers of *C. gemellata* were calculated as percentages of the total prey.

Dispersal and feeding periods of adults of *C. gemellata* was ascertained by marking 25 freshly-emerged individuals with red enamel from a pressurized container.

## RESULTS

The chrysomelids, *Chrysolina gemellata* and *C. hyperici*, under laboratory feeding tests, failed to show any preference for any one or more of the following species of *Hypericum*: *H. calycinum*, *H. frondosum*, *H. moserianum*, *H. olympicum*, *H. boreale*, *H. spathulatum*, *H. kalmianum* and *H. perforatum*. Life cycles of both chrysomelids were completed on green foliage of the first three of these as well as on that of *H. perforatum*. In considering the advisability of making releases of the beetles in British Columbia, the harmful economic importance of the weed was regarded as much greater than the ornamental value of the cultivated species of *Hypericum*.

All colonies of *C. gemellata* and *C. hyperici* released in British Columbia prior to 1956 have become established. Only in the colony of *C. hyperici* at Fruitvale, however, has a considerable degree of control been achieved. Here, an area of approximately 400 square metres has been cleared of the weed during 1955 and 1956. The weed infestation occurs largely on a gravelly cut-bank of a railroad right-of-way. The environment is different from that in any other colony in that there is usually a good cover of snow in winter and sufficient precipitation during the summer to maintain some green foliage on the flower stalks. In this infestation the population density (18 per quarter-square-metre) of flowering stems of the weed was greater than in any of the other infestations.

The population density of *C. hyperici* at Edgewood, also, is increasing more rapidly than that of *C. gemellata*, though both insect species were established at the same time and under very similar conditions, namely deep gravel soil with excess drainage, extremes of temperatures, and some shelter from winds by surrounding forests.

Of the other established colonies of *C. gemellata*, that at Fife, though released a year later than those at Christina Lake and Westbank, has the highest population density. Situated only two miles east of Christina Lake, this colony was subjected to similar climatic and light conditions. The Fife colony was established on a loose, sandy



soil whereas that at Christina Lake was on a stony silt with numerous limestone and granite outcrops. The population of *C. gemellata* at Westbank has increased slowly in a habitat with the heaviest silt soil, the highest annual mean temperature and the lowest precipitation of any of the study areas. At Waldo, under soil and climatic conditions comparable to those at Edgewood, *C. gemellata* has become established but failed to bring about any appreciable control of *H. perforatum*.

The relative unimportance of the size of the initial releases was demonstrated at Fife where only 3,000 adults were released in comparison with 5,000 at each of Christina Lake and Westbank, 12,500 at Edgewood, and 36,000 at Waldo. Moreover, the original colony of *C. hyperici* at Fruitvale, consisted of only 200 individuals.

No attempt was made in 1956 to determine the extent of establishment of the root borer, *A. hyperici*, at Christina Lake because of the danger of disturbing an already weak colony. The cecidomyiid, *Zeuxidiplosis giardi*, was found commonly in 1955 in the vicinity of the release site but was apparently annihilated by sudden sub-zero temperatures in mid-November, 1955 as no galls could be found in 1956.

The surveys of *H. perforatum* and the two insect species, *C. gemellata*, and *C. hyperici*, were carried out in permanent, randomly selected quadrats because the beetles of the initial importations dispersed over large proportions of the individual infestations during the first season. In the infestations under investigation dense weed occurred only on areas of from 15,000 to 20,000 square metres which, except for that at Edgewood were isolated from one another by topographical barriers. In British Columbia there has been no mass movement of beetles in great waves of perhaps 10 metres in width, behind which the weed was completely defoliated, as in California and parts of Idaho. Instead, increases in population density have been consistently small throughout the main portions of the infestations.

The changes in the bulk or volume of *H. perforatum* from 1953 to 1956, inclusive, shown in Table I, were calculated from averaging the heights of all the flowering stalks in the randomized quadrats. Significant increases recorded since 1953 resulted from abnormal production and survival of seedlings during that year, presumably because of unusual climatic conditions: abnormal precipitation during the first six months and subnormal temperatures during June, July and August (when the seedlings usually perish from desiccation). Subsequent reproduction has been nil. Large numbers of plants of the 1953 crop, however, flowered for the first time in 1955 and 1956 and substantially increased the populations of flowering stalks above those of 1953. For the same reason, vast expansion of originally very small infestations of *H. perforatum* was evident in many areas, particularly in that part of the Kettle Valley that parallels the United States border. Presumably, at least in part, for this reason the recorded increases in the population of *C. gemellata* appeared relatively ineffective in controlling the weed.

TABLE I—Average Heights in Metres of Flowering Stalks of *H. perforatum* per Quarter-Square-Metre Quadrat at Different Localities in 1953-56.

Quadrat at Different Localities in 1953-56.					
	Average per quadrat 1953	Percentage change from previous year			1956 Average per quadrat
		1954	1955	1956	
<i>C. gemellata</i> colonies:					
Christina Lake	5.32	+ 13.7	+ 17.4	—16.8	5.89
Fife	1.64	+ 2.4	+ 63.1	—33.8	5.92
Westbank	2.91	+ 30.5	—19.6	+ 90.7	5.93
Edgewood	4.47	+ 87.3	— 4.3	—15.7	6.75
<i>C. hyperici</i> colonies					
Fruitvale	5.60	+ 34.6	+ 29.7	—11.1	8.69
Edgewood	0.29	+ 66.8	+ 224.6	+ 60.7	2.53

The substantial reduction in bulk of *H. perforatum* in most of the areas under study in 1956, as shown in Table I, was presumably the result of sub-zero temperatures



that occurred suddenly during the previous mid-November. The great increases recorded at Westbank and Edgewood were in areas of very low population density. The potential rate of spread of the weed in a very sparse infestation was demonstrated at Edgewood.

Of the 95 plant species found in the quadrats at Christina Lake, Kentucky bluegrass, *Poa pratensis* L., represented 35.2 per cent of the floral ground cover, compared to 16.6 per cent of *H. perforatum*, though the latter, by its greater height and bulk, superficially appeared the dominant species. Third in percentage floral coverage (5.8) was *Medicago lupulina* L. which has some value in soil improvement programmes. In the event of removal of *H. perforatum* from the habitat, *P. pratensis*, *M. lupulina*, *Trifolium repens* L., *Agropyron cristatum* (L.) Gaertn., *Melilotus alba* Desr., and other more economically useful species might be expected to increase.

Population surveys of *C. gemellata* and *C. hyperici* in only two of the six colonies investigated are reported here. An inadequate number of samples was taken in the other four colonies where population levels were low.

At Christina Lake populations of each metamorphic stage of *C. gemellata* were sampled in 300 quadrats each of 200 square centimetres. Percentage increases in populations over those of the previous years during 1955 and 1956 were as follows: (a) larvae: 629.0 and 54.2; (b) pupae: 429.0 and 36.5; (c) adults: 350.0 and 22.2.

Percentage increases in the *C. hyperici* colony at Fruitvale during the same two years were: (a) larvae: 133.3 and 408.0; (b) pupae: 300.0 and 116.2; (c) adults: 98.7 and 137.5.

The mean adult population per quadrat of 200 square centimetres in 1956 was 0.018 at Christina Lake and at Fruitvale 0.317 or approximately 17.6 times that at Christina Lake, thus at least in part accounting for the higher degree of control evident at Fruitvale. The colonies of *C. hyperici* in British Columbia have dispersed much more slowly than those of *C. gemellata*.

Peak populations of the various metamorphic stages of *C. gemellata* at Christina Lake in 1954 occurred on the following dates: first-instar larvae, April 23; second-instar larvae, May 3; third-instar larvae, May 14; fourth-instar larvae, May 20; pupae, June 1 and adults (in the soil), June 14. The earliest date of feeding by adults was June 11. Mating began on August 30, two weeks after the first of several days of rainfall.

Suspicion that ants are important mortality factors was dispelled by examination of all of the prey taken into the single known colony of *Formica rufa* group in the Christina Lake area. The freshly-emerged beetle adults were most vulnerable and represented from 14.5 to 29 per cent of totals of 60 or more insect specimens carried during four-hour periods. As sclerotization of the exoskeletons increased, however, percentages of prey that comprised adults of *C. gemellata* dropped to 4.5. Adult beetles were never intercepted on the ant trails after their emergence from aestivation. Populations of *C. gemellata*, and thus defoliated stems of *H. perforatum*, within the foraging area of this ant colony were greater than those in any other part of the study area, perhaps because carabids, cicindelids, and other insects predacious on the beetles were removed from the habitat by the ants.

Adults of *C. gemellata*, marked by paint soon after emergence from the soil, moved distances up to 1.8 metres. The longest feeding period prior to aestivation was 17 days. Adults of this species, imported to Christina Lake in 1951, moved southward 187 metres during the first autumn.

### ACKNOWLEDGMENTS

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### DISCUSSION

HENRY A. BESS. What about parasites or predators of the beetles?

J. MORRIS SMITH. No parasites or predators of importance have been observed on *Chrysolina* spp. in British Columbia, though freshly emerged adults of *C. gemellata* constituted 29 per cent of the prey insects carried into a nest of the ant, possibly *Formica obscuripes*, mentioned in the text. The older, chitonized adults were seldom attacked.

J. FRANZ. I should like to obtain additional information on the reasons for negative results in British Columbia. Are the maximum numbers of beetles per areal unit lower in British Columbia than in California?

J. MORRIS SMITH. The annual mean temperature of 62.7°F. at Christina Lake, B.C., is approximately 17°F. below that at Redding, Calif., near which *C. gemellata* was collected. Added to a much lower autumn rainfall than in California, these factors result in less fall growth and very little autumn development of larvae as found in California. Populations of *Chrysolina* spp. per unit area have never been as high as those in California or even in the adjoining state of Idaho. Mr. Holloway and Dr. Huffaker have views on these points.

JAMES K. HOLLOWAY. I think rainfall is more important than temperature in the control of Klamath weed because the synchronization of the insect with the plant is dependant on this.

CARL B. HUFFAKER. I believe that there is little correlation between the observed density of beetles and control. If the rainy and dry seasons are synchronized critically for the weed in relation to the cycle of the insects as well, then good control may be achieved by fairly low populations of beetles; whereas if this is not so, the weed may persist in abundance and maintain large populations of beetles year after year. I believe that temperature is a minor contributing factor.



# Neue Erfahrungen über Einwirkung der Roten Waldameise auf den Massenwechsel von Schadinsekten sowie einige methodische Verbesserungen bei ihrem praktischen Einsatz

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## ZUSAMMENFASSUNG

Ameisen stellen prinzipiell einen wichtigen Faktor bei der biologischen Regulierung von Insekten-Uebersvermehrungen dar.

In Deutschland liegen umfangreiche Erfahrungen mit der *Formica rufa*-Gruppe vor. Von Bedeutung ist die durch die Polygynie der Kleinen Roten Waldameise bedingte starke Reproduktionsfähigkeit; der starke Brutanfall mit seinem gesteigerten Eiweissbedarf erfordert erhöhte räuberische Tätigkeit. Zugleich ermöglicht die Polygynie eine künstliche Bildung beweiselter "Ableger".

Hinsichtlich des Nutzeffektes von *Formica rufa rufo-pratensis minor* gegenüber Schadinsekten sei folgendes herausgestellt: Die früheren Befunde wurden durch planmässige Untersuchungen bestätigt und erweitert. Die grösste Wirksamkeit ergibt sich gegen Lepidopteren und Tenthrediniden, rechtzeitige Ansiedlung von 4 Nestern pro ha vor Anlaufen der Massenvermehrung ermöglicht deren Unterdrückung. In erster Linie ist die Rote Waldameise jedoch nicht Mittel zur biologischen Bekämpfung, sondern zur Vorbeugung mittels biologischer Regulationsmassnahmen im Sinne der "Waldhygiene". Eine endgültige Beurteilung des Nutzens ist erst nach grossflächiger, einige hundert ha umfassende Ansiedlung der Roten Waldameise und nach dem Heranwachsen ihrer Kolonien zur vollen Wirkungsgrösse möglich.

Die Verfahren zur künstlichen Verbreitung und zum Einsatz wurden mit der *Formica rufa*-Gruppe biologisch und technisch bis zur Praxisreife durchentwickelt.

Die von unseren bedeutendsten alten Forstzoologen und Forstpraktikern immer wieder aufgestellten Behauptungen über den hervorragenden Nutzen der Roten Waldameise sind auch in den vergangenen Jahren durch neue Beobachtungen bestätigt worden. Durch grundlegende Studien über Rassenunterschiede konnten eine Kleine Rote Waldameise (*Formica rufa rufo-pratensis minor*), weniger Mittlere Rote Waldameise (*Formica rufa rufo-pratensis major*), als besonders wirkungsvoll herausgestellt werden. Zunächst sind im Gegensatz zur Grossen Roten Waldameise (*Formica rufa rufa*), welche nur über eine einzige Königin verfügt und daher in etwa 20 Jahren ausstirbt, die Kolonien der Kleinen Roten Waldameise und Mittleren Roten Waldameise potentiell unsterblich; denn sie verjüngen sich fortlaufend durch Adoption junger Königinnen, die im eigenen Nest nachgezogen werden können. Hinzu kommt, dass gerade die Nester der Mittleren und besonders der Kleinen Roten Waldameise sehr verträglich sind und infolgedessen der Wald lückenlos etwa im Abstand von 50 m oder noch enger mit Nestern dieser nützlichen Insektenräuber angereichert werden kann. Die Verträglichkeit selbst beruht auf dem durch den Königinnenreichtum der beiden nützlichen Rassen bedingten Mischgeruch, während die Kolonien der Grossen Roten Waldameise nach dem Duft der einzigen Königin ausgerichtet sind und daher untereinander sich nicht vertragen. Die Vielzahl der Königinnen bedingt zugleich eine ausserordentlich hohe Individuenzahl in den vielen Nestern, die eine Kolonie umfasst. Auf solche Weise steht der Massenentfaltung von Schadinsekten eine Massenwirkung nützlicher Ameisen gegenüber. Dabei ist diese Auswirkung der Waldameisen von anhaltender Dauer, nicht nur wegen der erwähnten potentiellen Unsterblichkeit der Kolonien, sondern zugleich jahreszeitlich zufolge ihres eigenen Klimahaushaltes. Ein eigener Nahrungshaushalt in Form von zuckerhaltigen Ausscheidungen der von den Ameisen besuchten Rindenläuse macht die Waldameisen unabhängig von den Schadinsekten als Nahrungsfaktor, so dass auch zu sonst insektenarmen Zeiten die auf engem Raum dicht gedrängten Kolonien ohne weiteres sich zu erhalten vermögen.

Bei der Wiederbesiedlung bisher insektengefährdeter Waldbestände nach 1945 durch die Rote Waldameise in über 30 verschiedenartigen Standorten hat sich zunächst gezeigt, dass nicht ein einziger Biotop enthalten war, in dem die Ansiedlung nicht gelungen wäre.

Zwei Kolonievermehrungsverfahren sind bisher praktisch erprobt: Nach Methode I werden aus Stamm-Kolonien in grosser Zahl Arbeiterinnen zusammen mit alten Königinnen entnommen. Für einen Ableger ca. 100,000 Arbeiterinnen, das sind aus dem dichtesten Ameisengewühl 4 Stück 50-Liter-Behälter und dazu kommen mindestens 200 alte Königinnen (bis zu 3,000 in einem Nest vorhanden). Diese Methode I ist jedoch nur möglich im zeitigen Frühjahr. Eine zweite Methode der Kolonievermehrung folgt jahreszeitlich im Anschluss an die Sonnungsperiode, wenn keine alten Königinnen mehr in der Nestkuppel angetroffen werden, da sie sich dann schon wieder tief in den Boden zurückgezogen haben. Dann werden die jungen Königinnen aus der Labortoriuszucht nach allmählicher Geruchsangleichung an bisher weisellose Ableger angeweiselt.

Das Aussetzen der Ableger erfolgt im Abstand von 50 m über einem Baumstrunk; das Ameisenmaterial wird locker über dürres, auf den Baumstrunk gelegtes Reisig ausgeschüttet. Da die Ameisen sonnige Plätze bevorzugen, ist es zweckmässig, mit der Ansiedlung vom sonnigen Wald- und Wegrand her zu beginnen und in den nächsten Jahren Reihe für Reihe immer tiefer gegen das Waldesinnere hinein nachfolgen zu lassen.

Sehr wichtig ist es, nicht nur die neu ausgesetzten Ableger sondern auch die alten Stamm-Kolonien der nützlichen Waldameisen zu schützen. Unbedingt erforderlich ist wenigstens jetzt noch der sofortige Schutz der jungen Ableger nach dem Aussetzen. Besonders bewährt hat sich eine Ganzmetallschutzhaube.

Zu den bisher bereits als Beute der Waldameisen bekannten Forstschädlingen wie Nonne (*Lymantria monacha*), Kieferneule (*Panolis flammea*), Kiefernspanner (*Bupalus piniarius*), Kiefernspinner (*Dendrolimus pini*), Kiefernbuschhornblattwespe (*Diprion pini*) u. a. wurden neu als Massenbeute der Ameisen in Versuchen erwiesen: Eichenwickler (*Tortrix viridana*), Lärchenminiermotte (*Coleophora laricella*) sowie die Kleine Fichtenblattwespe (*Lygaeonematus abietinum*). Bei jungen Ablegern betragen die Beuten von den 3 letztgenannten Schädlingen zwischen 5,000 und 25,000 Larven im Tag, bei alten Nestern, z. B. im Eichenwicklerschadgebiet, etwa 65,000—100,000 Raupen im Tag; desgleichen werden ausserordentlich zahlreich auch Puppen und Falter mancher Schädlinge eingeschleppt.

Durch Untersuchungen von Ameisen-Kröpfen in einem mittelstark befallenen Eichenwicklerschadgebiet, konnte nun festgestellt werden, dass etwa 40% der Ameisen, die äusserlich keine Beute nach Hause tragen, ihren Kropf mit zerkleinerter Eichenwicklernahrung gefüllt haben. Es zeigt sich also, dass mit Beutezählungen allein die Auswirkung der Ameisen nicht hinreichend erfasst werden kann und es dürfte daher die sicherste Methode sein, etwa durch Auszählung von Schädlingsskot während der ganzen Frasszeit der Schädlinge oder durch Auszählung von Eiern und anderen Stadien den tatsächlichen Verlauf des Massenwechsels im Ameisengebiet und in einem ökologisch gleichartigen Vergleichsgebiet festzustellen. Dabei muss auch der Einfluss der Witterung berücksichtigt werden, desgleichen die Tageszeit. Solche Beobachtungen haben aber bisher nur bedingten Wert, indem sie nämlich auf einen Anfangserfolg junger Ableger hinweisen können, nicht jedoch auf den Enderfolg grossflächig vermehrter und herangewachsener Kolonien.

Da es nicht möglich war, Mittel für eine umfangreichere Vermehrung der Roten Waldameise aufzubringen, konnten trotz zahlreicher Einzelerfolge noch nicht so grosse Waldflächen angesiedelt werden. In vielen Fällen sind die Ameisenflächen noch so klein, dass bei ausgedehntem Kahlfrass von Schädlingen zwischen vereinzelt Waldameisenkolonien einerseits und den vor allem schwieriger zu erbeutenden Schädlingen andererseits (Eichenwickler, Fichtenblattwespe, Lärchenminiermotte u. a.) kein natürliches Verhältnis besteht. Ferner ist zu beobachten, dass die vor einigen Jahren ausge-



setzten Ableger noch lange nicht zur vollen Wirkungsgrösse herangewachsen sind, sondern bei zuverlässigem Schutz der Nester wenigstens 5—10 Jahre vergehen. In der Zwischenzeit dürften sich aus den im Abstand von 50 m ausgesetzten Ablegern neue Nester gebildet haben, vor allem an sonnigen, gut durchlichteten Waldbeständen. Die Waldameisenvermehrung ist keine biologische Bekämpfung sondern Waldhygiene, d. h. bereits vor Ausbruch der Kalamität müssen in den zumeist bekannten Dauer-schadgebieten die Waldameisen rechtzeitig angesiedelt werden und zu ihrer höchsten Wirkungsgrösse herangewachsen sein.

Die Waldameisenvermehrung soll nicht einseitig betrieben werden, sondern im Zusammenhang mit allgemein waldhygienefördernden Massnahmen wie naturgemässen Waldbau, Singvogelschutz etc. vereinigt werden. Dabei trifft es sich sehr gut, dass gerade die besonders nützliche Kleine Rote Waldameise in den am meisten insektengefährdeten Nadelholzmonokulturen verbreitet ist und mit einer Abart auch in den ebenfalls stärker bedrohten Eichenwäldern vorkommt.

Die Methoden der Ameisenvermehrung wurden inzwischen weiterhin wissenschaftlich fundiert. Durch zahlreiche Vergleichsversuche hat es sich als zweckmässig erwiesen, unbedingt mindestens 200 Liter mit dicht gedrängtem Ameisenmaterial zusätzlich 200 Königinnen auf einem Ableger zu vereinigen, also nicht zu kleine Ableger auszusetzen.

Das Rückgrat einer Massenvermehrung von Waldameisen bildet die Königinnen-Zucht. Nur auserlesene Stämme der Kleinen Roten Waldameise und evtl. der Mittleren Roten Waldameise, letztere für ökologisch ungünstige, also für sehr feuchte und schattige Wälder, sollen zur Königinnen-Zucht verwendet werden. Dabei müssen sich die Zuchtstämme durch besonders intensives Wachstum ihrer Kolonien, also auch durch Nestaufteilung sowie durch Erbeutung in Schadgebieten ausgezeichnet haben, um allmählich eine Auslese zu ermöglichen. Eine besondere Schwierigkeit der Königinnen-Zucht ist die oft zeitlich und räumlich ungleichmässige Verteilung von Männchen- und Weibchen-Nestern. Es besteht bei Waldameisen die Gewohnheit in manchen Nestern im Frühjahr nur Männchen oder nur Weibchen heranzuziehen.

Der Unterschied in der Aufzucht von Vollweibchen im Frühjahr und von Arbeiterinnen im Sommer ist bei der Kleinen Roten Waldameise bedingt durch eine Verschiedenartigkeit in der Ernährung der Ovariolen in der Winterruhe einerseits und im Spätsommer und Sommer andererseits. Die "Wintereier", welche zuerst im Frühjahr abgelegt werden, enthalten ein Polplasma, das mit Ribonucleinsäuregehalt ausgezeichnet ist; aus solchen Eiern können bei entsprechender Aufzucht Vollweibchen entstehen. Die befruchteten Sommereier dagegen enthalten dieses Polplasma in so starker Ausprägung nicht; aus solchen Eiern gehen nur Arbeiterinnen hervor.

Im übrigen hat sich während dieser Versuche gezeigt, dass die Rote Waldameise ihren Entwicklungsrhythmus ändern kann, sie ist also im Gegensatz zur Schwarzgrauen Wegameise (*Lasius niger*), die während des Winters ihre überwinternden Larven während dieser Jahreszeit nicht weiter zur Reife bringt, durchaus in der Lage, bei entsprechenden Temperaturverhältnissen auch mitten im Winter Eier zu legen und diese aufzuziehen.

Von ebenso grosser Bedeutung für die Königinnen-Zucht wie der Unterschied in der Aufzucht von Vollweibchen und Arbeiterinnen ist die Verschiedenartigkeit des Geschlechtes, welches ja durch Befruchtung oder Nichtbefruchtung der Eier festgelegt wird. Serienversuche in einem Brückenthermostaten haben nun erwiesen, dass im Januar ausgegrabene Weibchen oberhalb von etwa 19 °C befruchtete Eier ablegen, aus denen sich also Weibchen entwickelten und unterhalb 19 °C unbefruchtete Eier, aus denen Männchen hervorgingen. Es scheint, dass niedrige Temperatur die Weibchen zwar zur Eiablage an sich befähigt, jedoch nicht zur Ablage befruchteter Eier, da die niedrige Temperatur nicht zur Aktivierung der Muskulatur der Samenpumpe ausreicht. In Uebereinstimmung mit 25 jährigen ökologischen Beobachtungen, denenzufolge regelmässig die besonders schattig gelegenen oder die schwächeren Nester mit geringerem eigenen Wärmehaushalt Männchen, die sonnig gelegenen und starken Nester dagegen

Weibchen lieferten, zeigten also auch die erwähnten Laboratoriumsversuche das gleiche Ergebnis. Daraufhin wurden im Freien Weibchennester vor der Sonnungsperiode mit grünem Fichtenreisig abgedeckt und die Folge war, dass in solchen Nestern nunmehr Männchen zur Reife gebracht wurden, so dass dadurch der Anteil von Männchen- und Weibchennestern in den Königinnen-Zuchtstationen geregelt werden kann.

Das Absammeln der jungen begatteten Königinnen in den Gefässen erfolgt nicht mehr wie früher mit einer Federpinzette, sondern zur Zeitersparnis möglichst automatisch. Nachdem Männchen und Weibchen einige Tage unter Einwirkung von etwa 27° C und Bestrahlung mit UR-Lampen in grossen Zuchtbehältern zusammen waren und die Masse der Weibchen die Flügel abgeworfen haben, werden diese Ameisen in einen anderen Behälter gebracht, in dem nun eine Vorauslese zwischen Entflügelten und mit Wahrscheinlichkeit begatteten Weibchen einerseits und noch geflügelten Weibchen und Männchen andererseits vor sich geht. Die begatteten Weibchen haben nämlich das Bestreben nun nicht mehr gegen das Licht hin, sondern zur Dunkelheit zu laufen, es werden daher an den Auslesekasten Erlenmeyer-Kolben angeschlossen, die dunkel zu halten sind. Die begatteten Weibchen begeben sich in diese Kolben hinein und können einfach abgenommen und in einen weiteren Behälter ausgeschüttet werden, aus dem sie nunmehr mit elektrisch betriebenen Insektensaugrohren in kürzester Zeit in grosser Zahl aufgenommen werden können, um in Königinnenversandtuben gebracht zu werden.

Eine Kontrolle, inwieweit die Begattung erfolgreich verlaufen ist, soll stets an Proben durchgeführt werden; denn es hat sich gezeigt, dass zwar ein Waldameisenmännchen hintereinander bis zu 13 und noch mehr Weibchen begatten kann, aber meist wird nur zweimal ein hinreichend grosses Quantum von Spermien übertragen, das für mehrere Jahre zur Befruchtung von Eiern ausreicht.

Die in den Spezialversandgläsern verschickten Königinnen werden nun nicht einfach in die Ableger hineingeschüttet, sondern sie kommen zunächst in Anweisungsgläser zusammen jeweils mit einer grösseren Anzahl von Arbeiterinnen des Ablegers. Zu 200 Königinnen werden etwa bis zu 500 Arbeiterinnen eines Ablegers gesetzt, am nächsten Tag 1,000 Arbeiterinnen und am übernächsten noch eine grössere Zahl hinzu und am 4. Tag kann man die mit den Arbeiterinnen zusammengewöhnten Königinnen in ein Loch, das in die Nestkuppel des Ablegers gegraben wurde, hineinschütten und das ganze wieder zudecken. Die Adoption geht nun vor allem bei niedriger Temperatur leicht vonstatten. Eine vereinfachte Möglichkeit zur Adoption ist gegeben, wenn die Ableger erst dann ausgesetzt werden müssen, sobald junge Königinnen zur Verfügung stehen. Man schüttet dann jeweils 50 bis 100 Königinnen auf den Boden des Ameisentransportimers und füllt dann das Arbeiterinnen-Material aus dem Stamm-Nest nach. Während des Ameisentransportes, der sich oft auf viele Kilometer hinzieht, erfolgt ebenfalls ein Zusammengewöhnen der jungen Königinnen mit den fremden Arbeiterinnen.

Eine dritte Methode der Kolonievermehrung wurde noch ausgearbeitet unter Verwendung von schlüpfbereiten Geschlechtstierpuppen oder frisch geschlüpften Männchen und Weibchen. Man kann ohne weiteres Arbeiterinnen aus fremden Nestern der Kleinen Roten Waldameise zu einem Ableger vereinigen und wenn nun Männchen- und Weibchen-Puppen, bzw. frisch geschlüpfte Männchen und Weibchen, die getrennt aufgezogen wurden, zu einem Ableger vereinigt werden und noch dazu durch Ueberdecken des Nestschutzes mit einer Stoffhaube ihr Abflug verhindert wird, findet die Begattung auf dem Nest bzw. im Nest selbst statt und es kommt von selbst zur Anreicherung von jungen Königinnen, ohne dass eine Anweisung notwendig wäre.

Eine vierte Methode unter Verwendung der weniger nützlichen Grossen Roten Waldameise durch Anweisung von Königinnen der Kleinen Roten Waldameise ist noch nicht genügend praktisch erprobt. Eine Anweisung von jungen Königinnen der Kleinen Roten Waldameise an Königinnen der Mittleren Roten Waldameise geht leichter vonstatten. Stets muss bei der Grossen Roten Waldameise dafür gesorgt werden, dass die Königin des Stamm-Nestes der Grossen Roten Waldameise nicht in den Ableger hineingerät, weil sonst niemals junge Königinnen der kleinen Form aufgenom-

men werden. Eine Adoption von Königinnen der Kleinen Roten Waldameise bei Arbeiterinnen der Wiesenameise erscheint nach bisherigen Ergebnissen aussichtslos.

Methodisch steht dem Grosseinsatz der Waldameisen nach Verfahren I und II gegen die Forstschädlinge zur Wiedergesundung unserer Wälder nichts im Wege. Dieser nachhaltige und vorbeugende Schutz bisher insektengefährdeter Waldgebiete vor Schadinsekten, wenigstens vieler besonders wichtiger Arten, ist gerade wegen der Dauerwirkung und Natürlichkeit billiger als Bekämpfungsverfahren, die stets wiederholt werden müssen.

Es ist zu wünschen, dass im Interesse der Wiedergesundung und Gesunderhaltung unserer Wälder von den durch langjährige Grundlagenforschung und praktische Erprobung hinreichend fundierten Möglichkeiten zum Wiedereinsatz der Roten Waldameise möglichst umfassend Gebrauch gemacht wird.



# The Artificial Establishment of Wood Ant Colonies for Biological Control in The Netherlands

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## ABSTRACT

The most suitable wood ant for biological control in the Netherlands is the polygynous and polydomous *Formica polycтена* Foerst. New colonies are preferably founded with workers only from existing colonies (Gösswald's method II). The new colonies are then queenless, and their hostility towards alien ants, even of the same species, usually prevents them from adopting sufficient queens when they are offered by the experimenter or when available around the nest in the swarming season. Investigation showed that mated queens (obtainable in large numbers in the swarming season) may nevertheless be introduced by two methods: (1) by releasing them on the nest during a period of natural tolerance in early spring, (2) by releasing them together with the workers when the colony is founded. The first method has the drawback that it is difficult to have large numbers of queens available in early spring; the second involves the risk of a large proportion of the adopted queens perishing through unknown causes in the first few months of the colonies' existence. Both drawbacks have so far prevented the application of these methods on a large scale.

Of the artificially founded colonies which had been established for more than three years, and which were considered as possessing sufficient queens, about 20 percent subsequently died out owing to unknown causes. These losses were compensated for by the increase in population of other artificially founded colonies.

## INTRODUCTION

The following is a much abridged account of studies which will be published in their entirety elsewhere.

Reference will be made to a form of the red wood ant as *Formica polycтена* (Foerst.) (Bondroit 1918, Betrem 1953). It belongs to the "*Formica rufa* group" of species. It shows certain resemblances to *Formica rufa rufo-pratensis major* Gössw. and to *F. r. rufo-pratensis minor* Gössw. (Gösswald 1941, 1952), and may even be identical with one of these forms. As long as that identity has not been definitely established, however, it seems best to retain the separate names. The name *F. polycтена* is used in Belgium and the Netherlands.

*F. polycтена* is a mound-building species, the mound consisting of dry vegetable material. In the earth under the mound is a system of passages and chambers which form the subterranean part of the nest. Most nests contain a number of queens, sometimes up to 1000 or more. They usually live in the subterranean part of the nest, except in early spring, when they come up to the dome, and, in sunny weather, are often found just under or on its southern slope. The colonies of this ant may become so large that branch nests have to be built, and the number of nests belonging to a single colony may vary from one to about one hundred (Quispel 1941).

## ARTIFICIAL ESTABLISHMENT OF NEW COLONIES

Gösswald (1952, 1955) has described two methods by which new colonies of his "major" and "minor" may be founded artificially, and they work equally well with *F. polycтена*. In both methods ants are collected from existing colonies and liberated at the new nesting site. As it is impossible to separate the workers from the material of the dome that material with the ants and brood mixed up with it, is taken and put into a bag, which is later shaken out on the new nesting site. It is not necessary to take ants from the same mother colony, for workers from different colonies when brought together under these circumstances will unite to form a single new colony without the slightest show of hostility. The two methods of founding new colonies only differ in the time at which the ants are collected from the mother colony. By the first



method this takes place in early spring, when the queens are in the dome of the nest. They are then taken together with the workers, and the new colony starts off with a number of queens.

An obvious disadvantage of this method, however, is that the reproductive capacity of the mother colony is reduced. According to the second method the ants are collected later in summer, when the queens are in the subterranean part of the nest and are, therefore, inaccessible. Thus the queen population of the mother colony is not depleted. The colony recuperates in a short time, and may yield two or even three lots of ants for new colonies in one summer. The new colonies founded in this way, however, are queenless, and they usually remain so. Their hostility towards alien ants, also of the same species, prevents them from adopting queens, even if large numbers of young queens are available near the nests in the swarming period of nearby nests. Young queens offered by the experimenter, even if taken from one of the mother colonies, are also usually refused.

This second way of founding a colony would, therefore, be useless, unless methods could be evolved for introducing queens, as has been done in beekeeping. For two reasons it seemed an attractive idea to seek such methods:—(1) Under natural conditions all but a very small fraction of the young queens leaving the nest in the swarming season perish before having reproduced. (See also Gösswald 1952h: 80). (2) As in *F. r. rufobratensis* (Gösswald 1942, 1952), the males and females of *F. polyctena* are easily collected before they leave the nests, and they mate readily in captivity. Thus large numbers of young, mated queens, which would otherwise be lost, can be made available for introduction into the queenless colonies.

### INTRODUCTION OF QUEENS

For testing the behaviour of colonies in the field towards queens, tubular cages were designed, with perforations through which the workers could pass, but the larger queens could not (Fig. 2). They were made of 35 mm. cinematographic film, after the emulsion had been removed. Such cages with one or two queens in each of them were placed in the dome of the nest, near the base. The workers could then pass through the perforations and demonstrate their hostility or otherwise towards the queens. In summer the queens were usually found dead within twelve hours. To make sure that they had not been killed by causes other than aggression by the workers, check specimens in special check cages were always placed beside the test queens. The check cages were double-walled and had perforations through which neither the workers nor the queens could pass (Fig. 1), so that the queens were perfectly safe from attack by the workers. When both the test and the check queens were found dead, it was concluded that other factors than aggression by the workers had been responsible. The experiment was then considered invalid.

Fig. 3 gives the results of a series of experiments on four different nests. Time is plotted on the horizontal scale. There is no vertical scale. Each belt of dots, lines, and arrows shows the results of experiments on one nest. The dots represent test queens that were killed within 24 hours. They are mainly found in summer. A little earlier in the season we find short lines of different lengths representing queens with survival periods of one, two, or three days. Going back still further we find arrows, indicating survival periods of four days or more (up to several weeks, some even two months). Survival periods of four days or more were considered as indicating tolerance towards alien queens. It appears, therefore, that there is a relatively tolerant period in winter and early spring, which more or less gradually merges into a period of intolerance in summer. The wavy lines indicate the tolerant periods. Similar results were obtained in successive years, so that we find a regular alternation of tolerant and intolerant phases. Nest no. 180 in Fig. 3 was an exception; it showed no distinct tolerant period. A few more, similar exceptions were found.

Further proof of tolerance in winter and early spring was obtained by releasing queens in the periods indicated by the wavy lines, and recapturing them in the following spring, a year later. Before being released they had been marked by amputation of a few joints of one of the antennae. In 12 cases the average percentage of queens recaptured was 32. There was only one complete failure in which

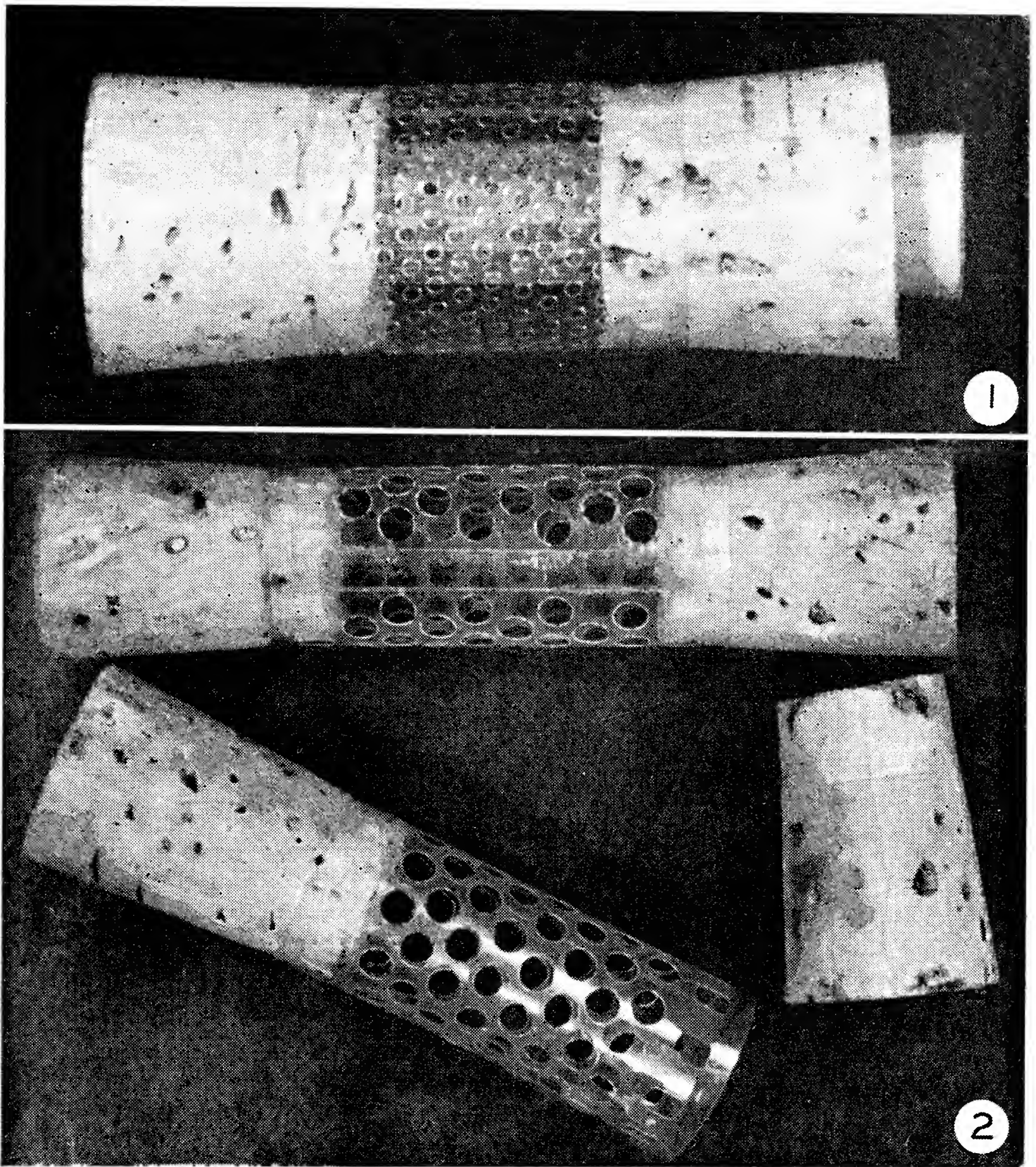


Fig. 1. Check cages for tolerance experiments.

Fig. 2. Test cages for tolerance experiments.

not one was recaptured. The highest number of recaptured queens was 72 per cent. Considering that it is unlikely for all the queens of a colony to be found when the nest is searched, it is almost certain that the numbers actually adopted are greater than these figures would suggest. The results also show that queens offered in the "tolerant period" are not only tolerated but also fed by the workers, i.e. they are actually received into the colony as members, or they would not have been found alive about one year later.

As to the causes of tolerance in this season, low temperature is certainly one of them. It is suspected, however, that other factors are involved as well.

At first sight the introduction of queens during the tolerant phase seems to be the solution to the problem. Unfortunately, however, it is difficult to have large numbers of queens available at that period, which occurs just before the swarming season. For that purpose they would have to be kept with worker ants in artificial nests from the swarming season of the previous year, i.e. for 8-12 months, which entails much

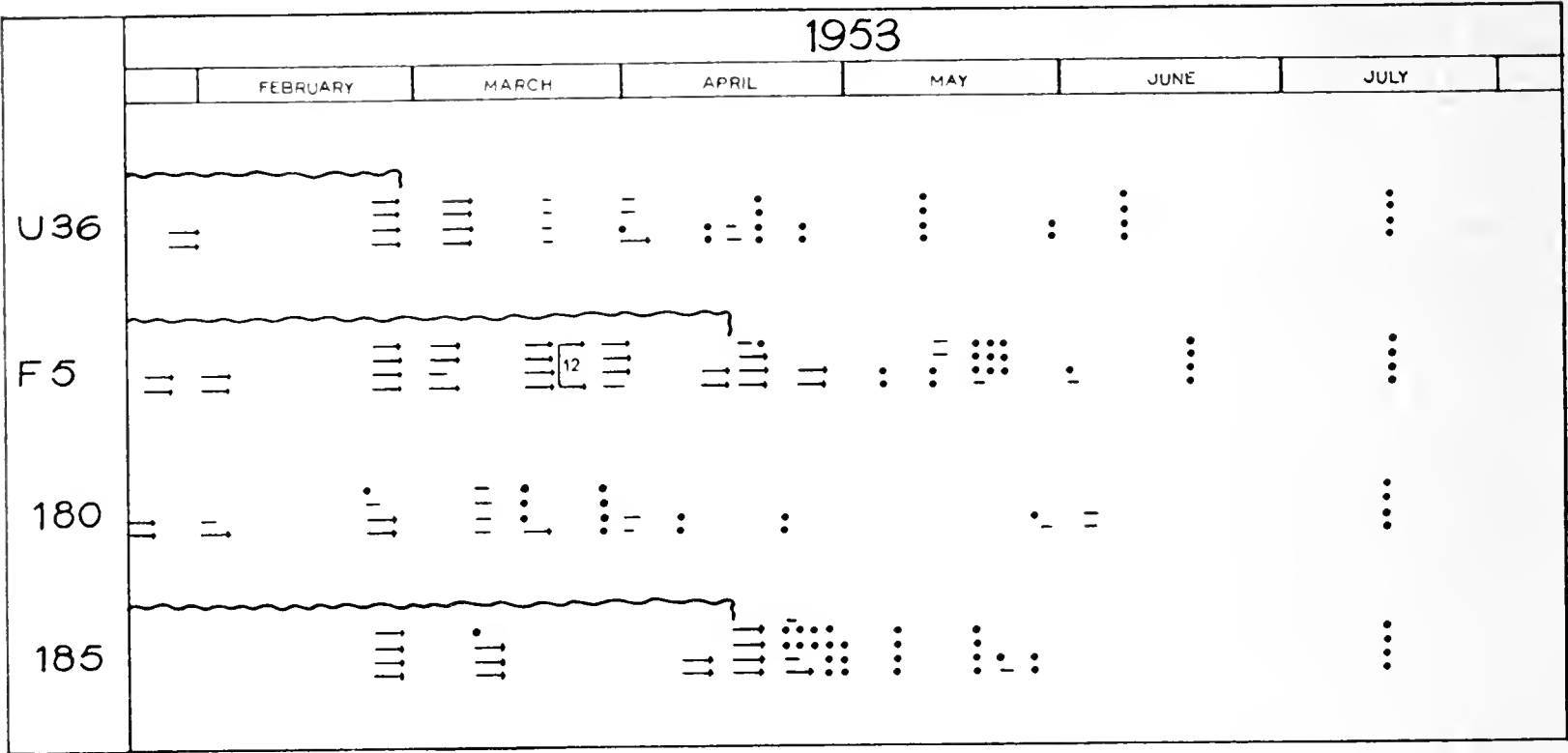


Fig. 3. Tolerance of field colonies towards queens in early spring.

labour. Also mortality among both queens and workers after several months in the artificial nests is often high. An additional difficulty is that to obviate the risk of releasing these carefully tended queens on exceptional, intolerant nests, all such nests would have to be tested, for tolerance first, which again involves extra labour.

Subsequent research was, therefore, directed towards another possible method of introducing queens. It has already been observed that worker ants from different colonies, when brought together in an unfamiliar environment show no aggressive behaviour towards one another. Experiments with the cages already described proved that under these conditions queens are also left unmolested.

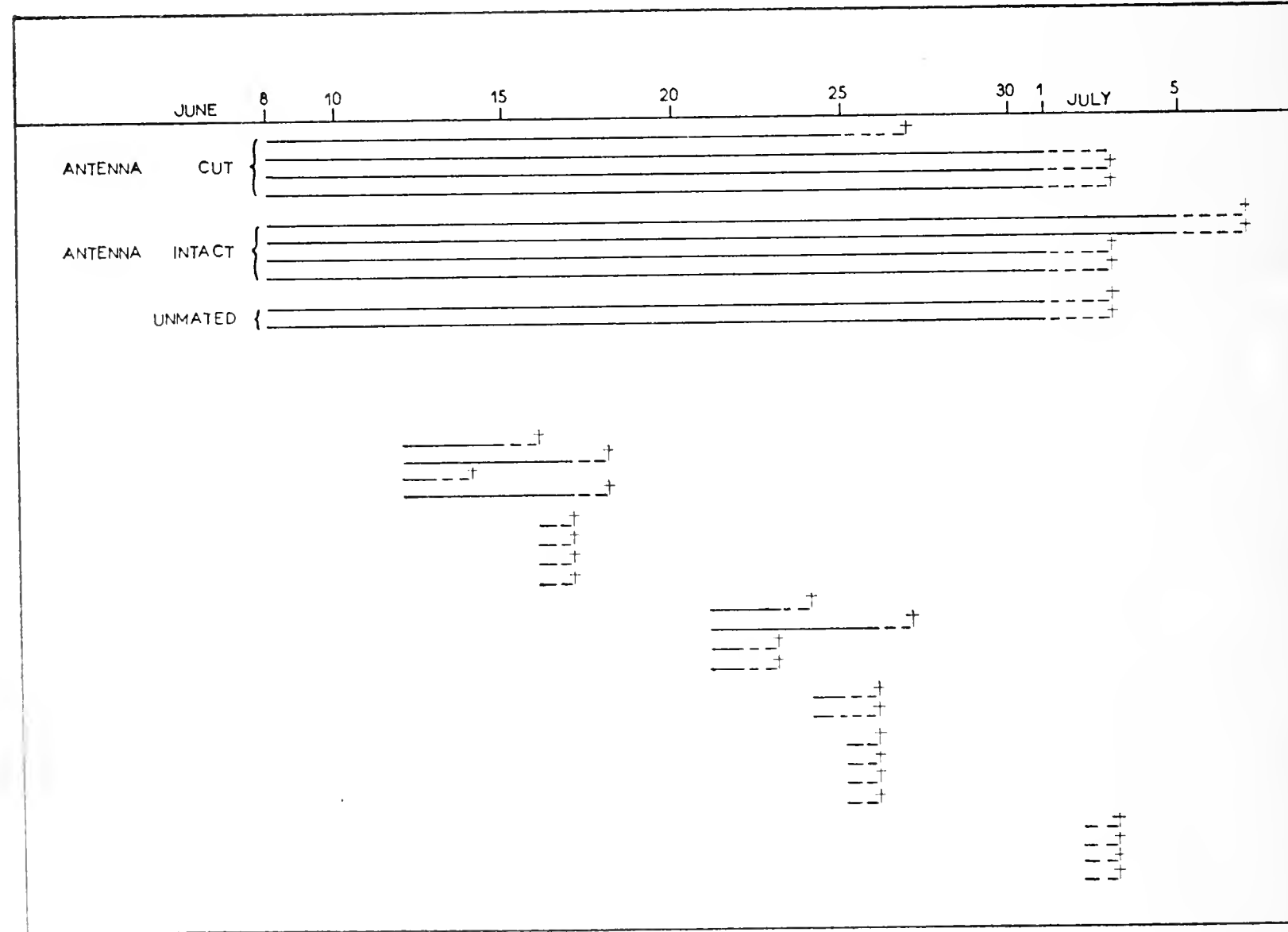


Fig. 4. Tolerance towards queens of newly established colony.



Fig. 4 gives the results of a series of experiments with a colony which was founded with workers from different mother colonies on June 8, 1954. This diagram differs from Fig. 3 in that all survival periods are given in full, also those exceeding four days. The dotted parts of the lines show the periods between two inspections during which the queens died. It appears that those offered on the first day remained alive for periods varying from 17 to 27 days, which means that they were accepted as members of the new colony. Incidentally, the figure also shows that mated and virgin queens are equally acceptable, and that mutilation of one of the antennae also does not affect their acceptability.)

It should be explained here that under normal conditions queens of *F. polystena* would live much longer, at least two years, probably longer. Confinement in the test cages apparently reduces their life-span considerably. Experiments with marked queens released on the nests, however, had shown that survival periods in the cages of only a few days were a reliable indication of the acceptability of a queen.

It further appears from Fig. 4 that the queens offered later survived for ever shorter periods, until we finally find that they are killed within one day, which is the normal condition in summer. There is apparently a short period of tolerance towards alien queens just after the colony has been founded.

In these experiments, too, marked queens were liberated on the first day, together with the workers. In 16 cases the average percentage of recaptured queens was 15; there were four cases of zero per cent, and the maximum was 52 per cent (one case). These figures are disappointingly low in themselves, and as compared with those for the tolerant phase. Neither are they in agreement with the results of the cage experiments. It seems likely, therefore, that the queens were initially received into the colonies but perished later. Nothing definite is known of how these queens met their end. However, one would be inclined to attribute their death, directly or indirectly, to the colonies not being quite normal in the first few months of their existence; for if queens are introduced during the tolerant phase later on, larger percentages are adopted. This second method of introducing queens, therefore, although probably based on a sound principle, involves a fairly great risk of failure.

The present situation with regard to queen introduction, therefore, is one in which we have two methods at our disposal. Both have their drawbacks which prevent them from being applied on a large scale. On a modest scale, however, the two methods may be and have been used to increase the ant population in coniferous plantations.

### VIABILITY OF ARTIFICIALLY FOUNDED COLONIES

The mere presence of sufficient queens is no guarantee that a colony will remain permanently established. Out of 43 colonies considered as possessing sufficient queens and believed to have been started in suitable environments, 13, that is about 30 per cent died out in subsequent years. It might be preferable to consider only colonies that have had sufficient opportunity to prove that they are capable of living in their new environment, and to show that they have overcome the effects of transplantation, e.g., colonies that have been established for more than three years. Of the latter, 20 per cent subsequently died out.

Not much is known of the causes of mortality. Predation by woodpeckers during hibernation can be excluded, for the nests concerned were always protected by wire netting in winter. The only disturbance they suffered from humans was very slight and occasional. It took place for the sake of ascertaining the presence of brood, and it is highly improbable that it seriously affected any of the colonies. In some cases the decline in numbers prior to the extinction of the colony was accompanied by the appearance of pseudogynes or of numerous staphylinid larvae (either *Atemeles* sp. or *Lomechusa strumosa* (Grav.)). Similar phenomena were also observed in natural colonies which subsequently died out.

Although sufficiently accurate data for drawing a comparison between the death rates of natural colonies and artificially-founded colonies are not available, it is believed that the death rate of the latter, if anything, is not much higher than that of the former and that the loss of a certain number of artificially-founded colonies is unavoidable.

In any case, so far, these losses have been compensated for by the increase in size of other artificially-founded colonies, some of which have established branch nests and have become fair-sized polydomous colonies.

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### DISCUSSION

HENRY A. BESS. In referring to the beneficial effects of the ants you mention the lesser damage by aphids than by others. How was the damage measured or assessed?

E. T. G. ELTON. I did not investigate that point myself, but relied on the literature.

M. J. WAY. Although this is not strictly relevant to the subject, do you know what harm is done by the ant-attended aphids? In my work I have noticed young trees being seriously damaged but older trees apparently did not suffer severely.

E. T. G. ELTON. The harm done by the ant-attended aphids is hardly noticeable, and generally considered of no importance as compared to the beneficial effect of the ants.

M. J. WAY. Do you know why natural colonies have not developed in areas where artificial establishment is successful?

T. T. G. ELTON. Spread of the species is extremely slow. The artificial establishment of colonies merely serves to speed up the natural invasion by ants of coniferous plantations. These are usually established on sites where no conifers grew previously.

P. B. DOWDEN. Is colonization of ants helped by correlating this work with abundant host populations?

E. T. G. ELTON. No correlation necessary because ants will bring in sufficient aphids to supply food as honey dew.



# The Role of the Ant in the Biological Control of Scale Insects in California<sup>1</sup>

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## ABSTRACT

In California economically important ant-induced outbreaks of homopterous insects are largely limited to plants on which the Argentine ant, *Iridomyrmex humilis* Mayr., is attending the citrus mealybug, *Planococcus citri* (Risso).

Ant-induced outbreaks of coccids occur with species generally held at low densities by natural enemies whose reproductivity is adversely affected by ants. The natural enemies of a coccid are classified according to their reproductivity as affected by ant activity, such reproductivity being unaffected, retarded, or enhanced. Most ant-induced outbreaks of a homopterous insect are highly localized and exist for only a few months or years. Ant-induced outbreaks may be of value in preventing violent fluctuations in the populations of a coccid, since they tend to maintain a more constant population of natural enemies.

Man and the ant have much in common, both being social creatures, both being omnivorous, and both inhabiting the same general environment. Under these circumstances it is inevitable that certain conflicts of interest should arise. An instance occurred upon the accidental introduction of the ant *Pheidole megacephala* (F.) into the Hawaiian Islands, where it exterminated some of the interesting island fauna and aroused the ire of both naturalist and taxonomist (Perkins, 1913; Williams, 1931). The ant, because of its entomophagous habits, is said to head the list of insects that are beneficial to man (McCook, 1882). It appears, in fact, that ants in the aggregate destroy vast numbers of noxious insects and that the economic value of the ant in this respect has been generally underestimated (Delpino, 1874; Clausen, 1940).

Observations on the predatory action of ants against phytophagous insects have shown that such action is usually intensified when the plants possess extra-floral nectaries or are more or less infested with homopterous insects that produce a honeydew of a quality attractive to ants, the increased predatory action on such plants resulting from the consequent concentration of the ant population. For example, control of the codling moth by ants is more effective on apple trees infested with aphids than on trees without aphids (Jaynes and Marucci, 1947). In the forests of Germany the population of the predatory ant *Formica rufa* L. is increased by artificially established nests. A correlated increase in the number of aphid-infested plants follows the increase of the ant population. According to Müller (1955), the possibility of damage from large aphid infestations must be considered in thus utilizing *F. rufa*, particularly in pure stands of timber. He has pointed out in this connection that any damage caused by aphids must be reckoned as the price paid for the predatory work of the ants.

Under certain circumstances the price of this beneficial action of ants may be too high. Instances of this have occurred in California with homopterous agricultural pests that are generally controlled by natural enemies. Outbreaks of such pests occur when the reproductivity of their natural enemies is markedly depressed by the activity of ants. In other words, the natural enemies must keep the pest population in general greatly reduced if the ants attending the pest are to be the cause of outbreaks of economic importance. The incidence of such outbreaks depends on the susceptibility of the effective natural enemies to ant activity. This susceptibility differs with different species. According to Horton (1918), the reproductivity of parasites is less depressed than that of predators. H. Compere (unpublished notes) observed, however, that the coccinellids *Rhizobius ventralis* (Er.), *Chilocorus bivulnerus* Muls., and *Olla abdominalis* (Say) are able to prey on the black scale, *Saisettia oleae* (Bern.), when the latter is heavily attended by ants.

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The natural enemies of homopterous insects may be classified according to the reproductivity of their populations as influenced by ant activity. On this basis species of natural enemies are designated as reproductively unaffected, reproductively retarded, or reproductively enhanced.

The reproductively unaffected species are represented by *Tetracnemus pretiosus* Timb. The mealybug hosts, *Pseudococcus gahani* (Green) and *P. aurilanus* (Mask.), were very abundant in California prior to the introduction of this parasite from Australia in 1927. Since *T. pretiosus* became established, there have been no ant-induced outbreaks of these mealybugs, although they produce a honeydew that is attractive to ants. A similar situation exists with respect to *Rodolia cardinalis* (Muls.) and *Cryptochaetum iceryae* (Will.), the effective natural enemies of cottony cushion scale.

The reproductively retarded species are represented by *Metaphycus luteolus* (Timb.), the effective parasite of the soft scale, *Coccus hesperidum* L.; *M. helvolus* (Comp.), the effective parasite of the black scale, *S. oleae*; and the effective complex of predators and parasites of the citrus mealybug, *Planococcus citri* (Risso). *Coccophagus gurneyi* Comp., an effective parasite of *P. gahani*, may belong to this group, since experiments by Compere and Smith (1932) show that in oviposition it is subject to interference by ants. Ant-induced outbreaks of *P. gahani* are precluded by the coexistence of another effective parasite, *T. pretiosus*, whose reproductivity is unaffected by ant activity.

The reproductively enhanced species are represented by *Coccophagus rusti* Comp. and *C. capensis* Comp., parasitic on the black scale, and by *C. scutellaris* (Dalm.) and *Metaphycus stanleyi* Comp., parasitic on the soft scale. These four parasites reproduce more or less readily on hosts that are attended by ants. The host populations of such species necessarily are those that are under general control by more effective parasites whose reproductivity is inhibited by ants. The reproductivity of these four species is enhanced when as a result of ant activity the host population is increased. *Coccophagus capensis* Comp. has been observed to destroy completely a very heavy ant-created population of black scale in spite of the fact that that population was being attended by a dense population of the Argentine ant, *Iridomyrmex humilis* Mayr. Reproductively enhanced species are likely to reproduce less readily on host populations at low densities than the parasitic species in the other two classifications, presumably because they are less efficient in searching.

In California there are no records of economically important ant-induced outbreaks of homopterous insects prior to the introduction of the Argentine ant, an accidental introduction that occurred about 1900. Prior to 1915 the control recommendation to growers troubled with ants that were attending scale insects, aphids, and mealybugs was to spray or fumigate the ant-attended insects so that the ants would disappear (Wickson, 1904). Since that time, the recommendation has been just the reverse, that is, to poison the ants so that the ant-attended insects would disappear. By 1915 the Argentine ant had spread throughout the citrus area from Los Angeles to Riverside. Shortly thereafter R. S. Woglum (Smith, 1917; Woglum, 1942) demonstrated experimentally that outbreaks of the soft scale and the citrus mealybug were induced by the activity of the Argentine ant, an activity that interfered with the controlling effect of *M. luteolus* on soft scale, and of neuropterous, coleopterous, and dipterous predators on the mealybug. It is noteworthy that the introduction from Sicily in 1914 of the chalcid *Leptomastidea abnormis* (Gir.), an endoparasite of the citrus mealybug, was initiated because of the effect of the Argentine ant on the citrus mealybug predator complex. This parasite is observed only occasionally to give effective control of the citrus mealybug since such control usually occurs at very low host densities.

In California ant-induced economic outbreaks of homopterous insects appear to be limited to plants on which the Argentine ant is attending the mealybug *P. citri*. In the years immediately preceding the establishment of the Argentine ant in the citrus area of southern California, *P. citri* was often abundant on citrus in coastal areas which were still free of this ant, areas in which the predator *Cryptolaemus montrouzieri*

(Muls.) and the parasite *L. abnormis* had not yet become well established (Essig, 1910; Basinger, 1931). There is no record of any ants attending these infestations, although great amounts of honeydew were produced. Outbreaks of *P. citri* not induced by ants are now relatively rare, such outbreaks being observed most frequently in San Diego County.

During the summer and fall of 1917, C. P. Clausen (California Insectary note No. 1630) observed *P. citri* and its natural enemies in relation to ants in a 5-acre citrus grove in the Arroyo Seco, Pasadena. He concluded that the ants which were present in quite large numbers did not entirely prevent the parasite *L. abnormis* and the predators *Chrysopa californica* Coq., *C. montrouzieri*, *Hyperaspis lateralis* Muls., *Leucopis bella* Loew, *Sympherobius barberi* Banks and *S. californicus* Banks from destroying the mealybug.

Ant-induced outbreaks of coccids usually exist for a period of less than a year, except in situations where edaphic conditions are conducive to high, more or less permanent ant populations. For a period of 20 years the Argentine ant has been responsible for the large populations of black scale, *S. oleae*, chronically infesting plants of the *Baccharis pilularis* located within a mile of the seacoast from Santa Monica to San Francisco. The natural enemies known to reproduce on such ant-attended black scale are *Coccophagus scutellaris*, *C. cowperi*, *C. lycimnia*, and *C. ochraceus*. The scale, nevertheless, may kill the infested parts of the plant.

Currently the Argentine ant is being utilized by the Fillmore Citrus Protective District in maintaining on host plants in outdoor cages constant infestations of black scale free of natural enemies. These infestations serve as a source of very clean "seed" scale needed for the continuous mass culture of the parasite *M. helvolus*, several millions of which are released annually in the citrus orchards of the district.

The intensity of ant attendance on a honeydew-producing population varies inversely with the size of that population (Smith and Armitage, 1931). In the temperate zone the influence of ant attendance is at its maximum during the spring months. As the honeydew-producing populations increased in relation to the number of ants, the "protective" influence of the latter decreases until the natural enemies, particularly the parasitic forms, are able to increase and reduce the populations of their hosts. This process is hastened with the approach of winter and the lowering of soil temperatures, the consequent decrease in ant activity then being relatively greater than the decrease in activity of the natural enemies.

The natural enemies of honeydew-producing insects may exert a regulating influence on the abundance of honeydew-feeding ants. This was demonstrated in California with black scale. Prior to the establishment of effective parasites of this scale (Compere, 1940), the ants had no influence on its abundance, but the abundance of scale and the large quantities of honeydew it produced markedly affected the abundance of ants. Black scale existed in southern California in large numbers on all its host plants (Smith and Compere, 1928) until the introduction and establishment in 1937 of the South African parasite *M. helvolus*. The reduction in black scale populations caused by the parasite resulted in a great reduction of the ant populations. This was strikingly demonstrated in the vicinity of Fillmore, California, where heavy infestations of black scale on the native shrub, *Rhus laurina* (Nutt.), were attended by the Argentine ant in very great numbers.

In the dry inland regions of California the succulent branches of the oleander, when lying on the ground and covered with leaves or debris, are exposed to a minimum of light, temperature, and desiccation, and thus form a highly favorable environment for the development of black scale. Such a cryptic environment is not suitable for parasitization of the scale by *M. helvolus*. It is highly suitable, however, for the co-existing, less effective South African parasite *C. rusti*. This parasite, working among the attending ants, exerts some control on the black scale, but this control is not accomplished as quickly or effectively as that by *M. helvolus*, which works only on the exposed parts of the plant. The progeny of such an infestation continuously infest the exposed portions of the plant.

It is evident that ant-induced infestations of coccids, if not too large, may have a beneficial function in that the dispersed progeny of such infestations tends to maintain

more or less constant populations of natural enemies, and these prevent extreme fluctuations in the coccid populations (Flanders, 1949).

Ant attendance on coccid populations may determine the composition of the parasitic fauna of such populations. With ant-attended populations of the soft scale, for example, the dominant parasite may be either *M. stanleyi* or *C. scutellaris*, not the generally effective species *M. luteolus*. Coccid-attending ants tend to clean the coccid-inhabited area of all dirt, debris, and miscellaneous organisms whether detrimental or otherwise. This cleaning may be done to the same degree as in the ant nest. In order that ants may not interfere with the establishment of natural enemies in a new habitat, the releases of newly introduced species are made only under conditions free of ants and other predators such as spiders.

The increase of a homopterous insect in the presence of ants and the invariable destruction of such ant-induced populations by natural enemies when the ants are artificially eliminated certainly demonstrate the effectiveness of such natural enemies. We can logically conclude from such a demonstration that the scarcity of the coccid within the geographical area concerned is an effect of natural enemies although not necessarily of the particular species that destroy the ant-induced infestations.

This phenomenon has been utilized in California in evaluating the possibilities of foreign exploration for the effective natural enemies of coccid pests. The observations of C. P. Lounsbury that the black scale in South Africa was nowhere abundant until after the introduction of the Argentine ant, and that the outbreaks of black scale occurring thereafter were associated with this ant, were considered by Smith and Compere (1928) as evidence that the generally low numerical status of black scale in South Africa is an effect of natural enemies. This conclusion has been substantiated by the effectiveness in California of parasites introduced from South Africa.

In South China the California red scale, *Aonidiella aurantii* (Mask.), apparently becomes abundant on orange only when the trees are frequented by the leaf-nesting ant, *Oecophylla smaragdina* F. We conclude, therefore, that the scarcity of the scale is an effect of its natural enemies. The nests of *O. smaragdina* are placed on citrus trees by the Chinese farmer on the assumption that it is effective in reducing citrus-feeding bugs and caterpillars. In 1948, J. L. Gressitt, then of Lingnan University, Canton, China, made a series of observations in an ant-inoculated orange grove at Lo-Kong-Tung, 23 miles from the University Campus, which showed that the red scale infestation was definitely influenced by this ant. When the utilization of the ants by the farmers was discontinued because of the Japanese occupation, the natural enemies, including the chalcid *Casca chinensis* How., controlled the red scale (J. L. Gressitt, unpublished notes).

Since the California red scale in South China is rarely abundant and since its scarcity is correlated with the presence of natural enemies, the introduction of these natural enemies is part of the biological control program of the University of California. A generally effective species or complex of species is yet to become established (Smith and Flanders, 1950). Meanwhile the occurrence of heavy infestations of red scale is usually unrelated to the presence of ants. In certain limited areas, however, red scale appears to be controlled by natural enemies since in such areas ant activity may cause "outbreaks."

The fact that the population density of coccids which do not produce honeydew may be as readily increased by ant activity as that of coccids which do has been demonstrated experimentally (Flanders, 1945) with the yellow scale, *Aonidiella citrina* (Coq.) (see Table I).

The populations of yellow scale in California prior to the introduction of *Comperiella bifasciata* How. were unaffected by ants. Ant-induced outbreaks of yellow scale are now possible because of the general reduction of yellow scale by *C. bifasciata* and because the reproductivity of this parasite is readily depressed by ant activity. The susceptibility of *C. bifasciata* to ant interference is an effect of its need to host-feed when adult and of its slowness in depositing its eggs, both functions being subject to interruption by ant activity.



TABLE I—Effect of Argentine Ant Activity on Parasitization of the Yellow Scale, *Aonidiella citrina* (Coq.), by *Comperiella bifasciata* How. on Adjacent Orange Trees, Redlands, California, 1943-1945.\*

Condition of scales	Mortality of yellow scales on the most heavily infested leaves, 1945	
	31 leaves from ant-free tree	31 leaves from ant-infested tree
Dead		
Parasitized	256	7
Nonparasitized	195	42
Alive	22	380
Total	473	429

\*In 1943 the test tree was freed of ants by the use of an ant Barrier. At this time both test and check trees were comparable in size and condition and both were equally infested with yellow and soft scales. The soft scales on the ant-free tree were completely destroyed within a few months by the parasite *Metaphycus stanleyi* (Comp.).

An ant-induced outbreak of a homopterous insect is a highly specialized phenomenon occurring with only a few of the species that are under control by natural enemies. The utilization of ants to measure the effectiveness of the natural enemies of coccids is of very limited application, since relatively few species of coccids are under control only by natural enemies whose reproductivity is so depressed by ant activity as to noticeably affect their densities.

The deliberate concentration of ant populations on plants very lightly infested with coccids, for the purpose of determining whether or not the low densities are an effect of natural enemies, has not been demonstrated in the field, but such a demonstration is certainly not impossible. Many coccids do not produce honeydew that is attractive to ants. A marked increase in the population of such species through the artificial concentration of ants would indicate the effectiveness of its natural enemies (DeBach, Fleschner, and Dietrick, 1951).

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### DISCUSSION

H. J. DE FLUITER. *Pseudococcus citri* is a serious pest on coffee in the Island of Ojava, Indonesia. It only occurs as a pest in the dry season. As soon as the wet season starts, the mealybug populations decrease rapidly by the action of parasitic fungi belonging to the genus *Empusa*. However, in colonies attended by *Anoplolepis longipes*, the mealybugs do increase even in the wet season. This implies that the ants prevent the infestation of the mealybugs by the fungus *Empusa*. I suppose that the ants do so by cleaning the mealybugs or even by eating the spores. Do you have any experience on this subject?

S. E. FLANDERS. *Pheidole* was more active during the wet season. I have not found fungi on *Pseudococcus citri*.

# Studies of Ants in West Virginia Apple Orchards

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## ABSTRACT

Ants were found to play an important role in reducing codling moth infestation in two apple orchards in West Virginia from 1938 to 1940. Eleven, of the 22 species found, attacked either naked codling moth larvae or larvae in the cocoon.

Experiments showed that 30 per cent or more of mature larvae released were attacked by predators within 24 hours. Ants were largely responsible for this mortality, especially *Formica fusca* var. *subsericea* Say. The cocoon stage is very vulnerable to attack by predators, particularly *Solenopsis molesta* (Say.), *Monomorium minimum* Buckley, *Aphaenogaster fulva aquia* (Buckley), and *Tetramorium caespitum* (L.).

A larger number of ant colonies were found in the biological control orchard, which had no cover sprays, than in the commercial orchard receiving 4 to 5 cover sprays. Tests made on plots in the biological orchard showed that spray adversely affected certain species of ants.

An attempt was made to increase the number and size of *Solenopsis* colonies by supplying grease in the form of lard and suet.

Studies of the effect that chemical control of the codling moth has on parasites and predators of this insect were made in two West Virginia apple orchards in 1938-40. The results of those studies were reported by Jaynes and Marucci in 1947. This paper will necessarily repeat some of that information, plus other observations not previously given.

In a biological-control orchard, the trunks and all main scaffold branches were banded with untreated 2-inch corrugated-cardboard bands. These bands were removed at 7- to 10-day intervals throughout the season and replaced with new bands. In a commercially sprayed orchard, all trees were banded with chemically treated bands except 20 study trees, which were banded with 2-inch strips of corrugated cardboard.

The biological-control orchard received a dormant or delayed-dormant oil spray, followed by a pink spray and a petal-fall spray. No cover sprays were applied to this orchard. The commercial orchard received a dormant or delayed-dormant oil spray, a pink spray, and a petal-fall spray each year; and in addition it had five cover sprays in 1938, four in 1939, and three in 1940.

Twenty-two species of ants were found in the two orchards during the three seasons, ten of which were fairly common. A brief note on the role each species plays as a predator of the codling moth as follows:—

*Solenopsis molesta* (Say) is a very important predator. It preys on codling moth larvae and pupae within the cocoon. It also attacks the larva while it is spinning its cocoon.

*Formica fusca* var. *subsericea* Say is also a very important predator. It preys on codling moth larvae seeking hibernation quarters. It also attacks larvae in the cocoon by making a large hole and withdrawing the larva. This species often injects formic acid into the larva in the cocoon, thus killing it; but then it fails to remove the larva.

*Formica pallide-fulva schaufussi incerta* Emery attacks larvae seeking hibernation and is much more active than *F. fusca*. But it is not so numerous.

*Aphaenogaster fulva aquia* (Buckley) attacks both larvae seeking hibernation and those within the cocoons. It is an important predator. Larvae released near a colony of *Aphaenogaster* were destroyed before they could make their cocoons.

*Tetramorium caespitum* (L.) attacks naked codling moth larvae, but does more damage when the larvae are making their cocoons or after they have completed them.

*Monomorium minimum* (Buckley) will attack larvae but are more important for preying on larvae with cocoons.

*Lasius niger alienus americanus* Emery and *L. niger* var. *neoniger* Emery do not prey on naked larvae; they attacked only those individuals that passed close to their nest entrance. No record was obtained of their attacking larvae within the cocoons.

*Pheidole pilifera* (Roger) is not an effective predator of naked larvae, as large numbers are required to subdue a larva. Nor is it an effective predator of larvae within the cocoon, though sometimes it makes holes in the cocoon and drags the larva out.

*Prenolepis imparis* (Say) is seasonal in its activity, being seen above ground only in the early spring and again in the fall. These ants do not attack codling moth cocoons (or at most only rarely), though they do occasionally attack a naked larva. This species must be rated on about a par with *L. niger*; it does not exert control of codling moth populations.

*Lasius* (*Acanthomyops*) *claviger* Roger was found to be fairly numerous in the biological orchard; but these ants lead a subterranean aphidicolous existence and therefore exert no influence on the codling moth population.

*Crematogaster lineolata* var. near *cerasi* (Fitch) do not kill codling moth larvae even when they pass very close to the colony site. These ants were occasionally found under the bands attacking a codling moth cocoon, or a larva in the process of spinning a cocoon in the biological-control orchard, although in all plots examined only two colonies were found and these were in the commercial orchard.

*Tapinoma sessile* (Say) occasionally attacks larvae within the cocoon but no record was obtained of its attacking naked larvae. Nine colonies were found in the two orchards.

*Formica truncicola* subsp. *integra* Nyl was not found in the plots examined for ants, but three colonies of this species were located and it was observed that these ants are also effective predators on larvae seeking hibernation.

*Myrmica scabrinodis sabuleti* Meinert does not attack either naked larvae or larvae within the cocoon. Codling moth larvae placed in the entrance holes to colonies of this species were unharmed. Eight colonies were found in the biological orchard and one in the commercial orchard.

*Formica pallide-fulva nitidiventris* Emery and *Formica fusca* var. *subaenescens* Emery probably attack larvae seeking hibernation as do the other *Formica* ants. Only two colonies of the former and one of the latter were found.

No record was obtained on the following species of ants encountered in the orchards as to whether or not they prey on the codling moth. Two colonies of *Polyergus lucidus* Mayr, two colonies of *Brachymyrmex heeri* subsp. *depilis* Emery, three colonies of *Brachymyrmex* sp., one colony of *Strumigenys reflexa* Wesson, and five colonies of *Lasius niger* var.

Killing of the codling moth larvae and pupae by predators in the corrugated-paper bands around the trunk and main lateral branches of 20 trees in each orchard averaged 4 to 14 percent for the two orchards in 3 years. However, between July 27 and August 25, 1939, the average rate of killing was 25 percent for the five times when the bands were removed. The greatest kill for any one date was 34 percent.

*S. molesta* was responsible for 38, 64, and 43 percent of this predation under bands in the biological-control orchard in 1938, 1939, and 1940 respectively. In the commercial orchard this species only accounted for 3, 42 and 5 percent in the corresponding years.

Tests showed that predation of codling moth cocoons placed on the soil or under trash was very close to 100 percent. In the spring and fall, carabid adults and larvae and *Chauliognathus* larvae were the major predators. During the summer, *Solenopsis* and *Monomorium* ants got over 50 percent of the cocoons. *A. f. aquia* and *T. caespitum* were occasionally found feeding on cocoons. Although *F. fusca* was never observed to attack cocoons, they made large holes to remove the larvae; they also killed the larvae without visibly damaging the cocoon.

To determine the relative population of predatory ants, a corresponding number of plots were examined each year in the two orchards. Each plot consisted of an area enclosed by four apple trees; it was carefully examined and all ant colonies were plotted. The first year 18 plots were examined in each orchard, 13 the next year, and 10 the last year.

The number of ant colonies recorded in the biological-control orchard was 159, 398, and 371 compared to 97, 291, and 236 in the commercial orchard for 1938, 1939, and 1940 respectively.

It was assumed that the smaller number of ant colonies in the commercial orchard was due to the cumulative effect of spraying, particularly with cover sprays.

This difference in the ant population in the two orchards becomes even more striking when the individual species are considered, also the time of year in which the plots are surveyed. There were always considerably more *F. fusca* colonies found in the biological-control orchard than in the commercial orchard. In 1938, nearly four times as many were found in the biological-control orchard. Those in the commercial orchard were all found in June.

*M. minimum* was much more numerous in the biological-control orchard in 1939 and 1940 than in the commercial orchard. *Aphaenogaster fulva* was much more numerous in the biological-control orchard all 3 years.

Approximately the same number of *Solenopsis* colonies were found in each orchard in 1938. However, very few colonies of this species were found in the commercial orchard after the middle of June. In 1939 the biological-control orchard had more ant colonies per plot than the commercial orchard. This difference was not so great as in 1938 because of an increase of *Solenopsis* colonies. This increase of ant colonies in the commercial orchard is reflected in the large percentage of predation obtained in that orchard in 1939. In 1940, the *Solenopsis* colonies found in the two orchards in July averaged the same. In May and June the biological-control orchard had averaged more, showing the greatest reduction of this species took place in the commercial orchard.

Comparing the number of ant colonies found during the three seasons, there was a slight increase each year in the biological-control orchard.

Four plots in each orchard, which were examined in June, were again examined in the middle of September to ascertain what changes had taken place in the number of ant colonies. The percentage of the total colonies recovered was 58 percent in both orchards. However, there was considerable difference in the relative recoveries of the different species. Seventy-five percent of the *S. molesta* colonies were recovered in the biological orchard as compared with only 54 percent in the commercial orchard. In the biological orchard, where *Aphaenogaster aquia* was always more numerous, only 42 percent were recovered; while in the commercial orchard, where *T. caespitum* was very abundant, only 55 percent of the colonies were recovered.

An attempt was made to measure the effect of spray material on ant colonies by sprinkling spray material on two plots in the biological orchard to correspond to what would have run off the foliage if they had been sprayed. It was estimated that the ground cover over the area of an ant plot would receive approximately 10 gallons of spray material at each spray operation. Spray material similar to three cover sprays used in the commercial orchard was applied by a hand sprinkler. These plots and two untreated plots in the biological-control orchard as well as two plots in the commercial orchard were examined in May and September for comparison of results. In addition two other plots in the biological-control orchard had spray sprinkled on one-half the area.

The total number of ant colonies found in the two untreated plots in the biological-control orchard and in the commercial orchard were approximately the same in September as in May. However, in the two plots in the biological-control orchard that were sprinkled with spray material there was a large reduction in the number of colonies found. There were only 56 colonies in September compared to the 90 colonies found in May.

There was a reduction of *Solenopsis* colonies in the sprayed and unsprayed plots of the biological-control orchard and the commercial orchard but the difference was not great enough to indicate any adverse effect of the spray.

*Aphaenogaster* apparently was affected seriously by the spray treatment in the biological-control plots, as there was a reduction of 64 percent between the September counts and those of the previous May; while in the other biological plots only a 28.5-percent reduction occurred. In the two plots where only half the area was sprayed, *Aphaenogaster* colonies increased from 6 to 10 in the unsprayed portions and decreased from 8 to 3 in the sprayed portions. *Tetramorium* colonies in the



unsprayed portion remained the same, there being 7 in May and September. However, in the sprayed portion there was a decrease from 10 colonies in May to only 1 in September.

From these small tests it appears that *Aphaenogaster* is considerably reduced by spray application, and it has been observed that this species was always more numerous in the biological-control orchard than in the commercially sprayed orchard. *Tetramorium* also appeared to be affected adversely by spray application. However, *Tetramorium* was more numerous in the commercial orchard than in the biological orchard. This may be due in a great measure to the association of the various species of ants and their inability to survive and increase when certain other species are present. It has been noted that in most cases where *Aphaenogaster* is present in large numbers *Tetramorium* is either absent or is present only in very small numbers.

An experiment was conducted in 1939 to determine if the number of *Solenopsis* colonies could be increased by increasing the food supply. Grease in the form of lard and suet was provided. It was found that lard between two layers of cotton fastened to the ground was the most practical method to use.

In two plots in each orchard, grease was placed from May 20 to June 15. On examining these later for *Solenopsis* colonies there was an increase of 11- and 18-fold in the biological and commercial orchard respectively. However, there was also a great increase of *Solenopsis* colonies in plots not given grease. In three plots in each orchard there was 4- and 11-fold increase in the biological and commercial orchard respectively.

These observations would indicate that the cover sprays had no apparent effect on *Solenopsis*. However, the second- and third-cover sprays this year had no nicotine or oil in them. On August 9, in the commercial orchard many dead *Solenopsis* were found on the surface of the ground around two colony sites. A commercial summer spray oil containing nicotine had been applied as a fourth cover on August 1.

Counts of ant colonies and a record of predation under corrugated bands showed that more ants and a great predation occurred in the biological-control orchard, which received no cover sprays, than in the commercial orchard. Observations and records of predation on released naked larvae and larvae in cocoons showed very clearly how important certain species of ants are as predators.

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## DISCUSSION

J. A. HALL. Does the total of ant predation on codling moth give sufficient control for economic production or sufficient that the number of applications of insecticide may be reduced?

H. A. JAYNES. Ant predation with other predation may give economic production with reduced spray application, if market available for the unsound fruit.

PAUL DEBACH. Was the food supply of ants greater in the biological plots than in the treated plots and, if so, could this account for the greater ant populations in the biological plots?

H. A. JAYNES. Yes. Percentage of sound fruit in the commercial orchard was 56, 70 and 75 as compared with 37, 38 and 28 in the biological orchard for 1938, 1939 and 1940 respectively. In the commercial orchard 72 per cent of harvest fruit was sound during the three years and in the biological orchard 50 per cent was sound.

D. W. CLANCY. How important was bird predation on overwintering codling moth larvae as compared with summer ant predation?

H. A. JAYNES. Not studied.

P. GARMAN. Effect of chlorinated hydrocarbons in ant populations: Has any work been done since introduction of chlorinated hydrocarbons?

H. A. JAYNES. No work.

M. J. WAY. Reference to effect of chlorinated orchards on ants: In work on eliminated *Anoplolepis* species which were abundant, nesting in the ground and foraging coconut plantations, I found that dieldrin dust applied to the palm crowns virtually in the trees. Application to the tree was more effective than application to the soil.



# The Effect of Ants on Citrus Scales at Letaba, South Africa<sup>1</sup>

By J. J. STEYN

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## ABSTRACT

A correlation project in plots distributed over the world's second largest citrus estate, incriminated the pugnacious ant (*Anoplolepis custodiens* Smith) as the cause of epidemics of red scale (*Aonidiella aurantii* Mask.) and soft scale (*Coccus hesperidum* L.). Some ant-infested trees dropped 500 oranges while many adjoining ant-free banded trees dropped none.

Ecological life history studies disclosed that the domestic economy of *Anoplolepis* is based on trees with honeydew-producing *Lecanium*.

Insectary rearings showed that a mean temperature increase of 1°C. (1.8°F.) shortens this ant's developmental period by 11.4% and increases scale control expenditure proportionately.

Feeding periodicity studies revealed statistically significant ant activity increases at increased temperature, increased light intensity, decreased humidity, and decreased barometric pressure, and that ant control along the two outside tree rows produced commercially scale-free plots.

*Anoplolepis* disturbed the following:—Parasites: *Aphytis chrysomphali* Mercet., *Apanteles* sp. and Predators: *Chilocorus distigma* Klg., *Chilocorus wahlbergi* Muls., other coccinellids, spiders.

Twenty-four consecutive hourly speed determination counts demonstrated a total ant patrol of 927,556 miles per day on a tree with an average of 1,000 ants on its trunk at one moment. This explains how efficiently *Anoplolepis* protects both scale species against their natural enemies, and causes epidemics.

A second project incriminated the cosmopolitan ant (*Pheidole megacephala* F.) as another cause of scale epidemics.

A third project demonstrated that ant patrol absence in plots with mixed populations of different ant species yielded scale-free trees.

Discing, vegetable cover, increased humus content, and bands of linseed oil plus DDT, were the most efficient ant control methods.

## INTRODUCTION

The present investigations were started by Mr. E. C. G. Bedford, who has succeeded the late Dr. G. C. Ulyett at the Parasite Laboratory, Pretoria, South Africa. During May and June, 1947, Drs. Ulyett and H. Compere worked with Mr. Bedford on the Letaba Citrus Estates. It appears that Flanders (1945) was the first to record a coincident infestation of a honeydew-producing coccid and a non honeydew-producing coccid, which was the result of the Argentine ant (*Iridomyrmex humilis* Mayr).

The new approach to the citrus red scale (*Aonidiella aurantii* Mask) problem, i.e.: controlling the ants which tended soft scale (*Coccus hesperidum* L.) for the sake of its honeydew, and caused red scale infestations, and thus leaving the direct control of the coccids to their natural enemies, led to 3 red scale-ant correlation projects.

**CORRELATION PROJECTS:** The first red scale-ant correlation project was laid out in 10 plots populated by the pugnacious ant (*Anoplolepis custodiens* Smith). These 10 plots were distributed throughout the Letaba Estates which is regarded as the second largest citrus estates in the world. Infestation categories for red scale, soft scale, defoliation, and ant infestation were devised to range from clean, light, medium, medium heavy and heavy. Only Valencia trees were used. In 4 plots the trees were 13 years old, and in 6 plots they were 30 years old.

Ants were kept out of experimental control trees by 2-inch-wide tanglefoot bands around the trunks, just below the crutches. Bands were checked every fortnight.

<sup>1</sup> Published with permission of the Directors of African Realty Trust.

Different experimental lay-outs were used for different plots, e.g. 2 rows of trees left ant-infested, and 2 rows kept ant-free by banding. The lowest and highest number of ant-infested trees used per plot were respectively 7 and 80 trees. The lowest and highest number of banded ant-free trees used per plot were 22 and 162.

The initial, average, red scale infestation of each of the 10 plots, ranged from very light to heavy. One plot was especially selected as it had not been fumigated or oil-sprayed for 4 years, because of its very light red scale infestation (less than 1 adult female red scale per fruit). Four plots were parts of half plots in which the original Navel trees were so severely damaged by scale insects that they had to be replanted with Valencias.

After 5 months of banding, defoliation occurred on some ant-infested trees in every experimental plot. The percentage of trees which defoliated, ranged from 6.7 to 65% of the ant-infested trees in the individual plots. In 8 out of the 10 plots, not one of the banded ant-free trees defoliated. In 2 plots 2.6 and 27.5% of the banded trees defoliated.

After 7 months the results were: In 5 of the 10 plots, not one ant-infested tree was commercially clean of red scale, i.e. had from 0.1 adult female red scale per fruit. In the other 5 plots only from 2.2% to 28.2% of the ant-infested trees were commercially clean. However, 59.0% to 100% of the banded trees in the different plots were commercially clean from scale after 7 months.

Further, detailed analyses of the results obtained from the 407 ant-infested and 554 banded trees used in these 10 plots, revealed that there was a marked correlation between the presence of *Anoplolepis* ants on citrus trees and red scale infestation.

In every experimental plot, ant-infested trees dropped fruit: From 71.4% to 100% of the ant-infested trees dropped fruit. In 2 plots not one banded tree dropped fruit. The average numbers of dropped fruit ranged from 0.09 to 10.6 per banded tree, and from 1.7 to 89.5 per ant-infested tree.

Soft scale infestations cleared up much more completely and much more readily than red scale infestations. This suggests that just as red scale decreased after soft scale decreased, red scale infestations followed only after soft scale increases. At the end of this project many hours were repeatedly used in searches to find soft scale on the 30-year-old banded trees, but virtually no soft scale was found, whereas red scale was still present in small numbers.

Some of the ant-infested trees dropped 500 oranges. Many of the banded trees dropped no fruit.

In one experimental plot the number of ants on the trunk of each tree at one moment was counted in groups of 5 ants, every Tuesday between 11 a.m. and 12 noon, for 1 year. The average percentage of dead wood caused by red scale and soft scale on each of these ant-infested trees, was calculated from estimates made by two men. In this plot an average of 40 ants caused 5% of dead wood, 80 ants caused 35% of dead wood, 120 ants caused 66% of dead wood, and 160 ants caused 96% of dead wood. A geometrical correlation was therefore found between the average number of ants on a tree trunk and the estimated percentage of dead wood caused by soft scale and red scale.

It was concluded that red scale and soft scale infestations on citrus were caused by the ant, *A. custodiens*, and that these infestations were annihilated by ant control.

Ant life-history studies were conducted. Twelve comparable nests were dug up every Monday, for 1 year. Similarly, in one plot the numbers of ants on the tree trunks of 45 trees were counted every Tuesday. The total number of larvae found in these nests revealed a very good correlation with the average number of ants on a tree trunk from August i.e. spring, to December i.e. midsummer. The total number of young larvae gave even a better correlation with the average number of ants on a tree trunk, and the medium larvae, which do most of the feeding, gave the best correlation.

In experimental Janet nests it was found that ant workers regurgitated honeydew to the ant larvae. Ant larvae were never fed with pieces of dead insects. It was concluded that the domestic economy of *Anoplolepis* is based on the trees on which it tends soft scale and aphids.

Simultaneously with the life-history studies made in the orchard, we also conducted insectary rearings in order to check deductions that would be made from field results. A thermograph was used in one of the experimental Janet nests. From this, 2-hourly temperature records were obtained.

It was determined that if an increase of  $1^{\circ}\text{C}$ . ( $1.8^{\circ}\text{F}$ .) in the average mean monthly temperature as recorded in a Stevenson screen effected a similar increase in the *Anoplolepis* nests, then this increase would have tentatively been expected to accelerate the development of eggs, larvae and pupae of minor worker ants by 2.7, 4.1 and 3.2 days respectively, and thus shorten the total development period by 10 days or 11.4%, thus causing total ant control expenditure to soar proportionately.

*Anoplolepis* workers are mainly diurnal and tend soft scale during the day. During the night, honeydew excreted by soft scale accumulates on the trees. In the early morning just before or just after sunrise, the ants imbibe so much honeydew that an ant which descends a tree trunk may weigh  $4\frac{1}{2}$  times as heavy as when it ascends the trunk.

On 7 trees we made hourly counts of ants on the trunks, for 24 successive hours. Temperature, humidity and light intensity records were made at the same time. This work was carried out on a dry day in midwinter, after a rainy night in midspring, on a dry day in midsummer, as well as on a rainy day in midautumn. Statistical analyses of these feeding periodicity studies on *Anoplolepis* revealed that ant activity is increased by increased temperature, by increased light intensity, by decreased humidity, and decreased barometric pressure.

Studies on temperature, humidity and light ranges in a plot led to the banding of only the 2 outside tree rows of plots. This produced commercially scale-free trees, not only on these 2 rows, but on most of the trees in the plots.

It is of general interest that some 30 years ago Professor F. S. Bodenheimer was sent by the Hebrew University of Jerusalem to Sinai, to determine whether the Biblical manna did fall or could not have fallen. He found that 2 scale insects which live on tamarisk trees, produce the manna. These coccids are tended by diurnal ants. I assume that Bodenheimer, who was the external examiner of my thesis on *Anoplolepis*, was interested in the statistical analyses of the feeding periodicity of this ant, as they readily explain why the Israelites had to collect manna in the early morning, i.e. before the ants started to work: also explain why the Israelites had to collect manna only for one day as a black fungus spoils the honeydew. With a little stretch of the imagination, it is also clear why manna fell in the desert and not in the Biblical Paradise.

When I started at Letaba the detailed, extensive and most thorough researches by Mr. Bedford, had revealed the following parasites and predators of red scale on the Estates: — Parasites: *Aphytis chrysomphali* Mercet, *Habrolepis rouxi* Compere. Predators: Coccinellids: *Chilocorus distigma* Klg., *C. wahlbergi* Muls., *Lotis neglecta* Muls., *Pharoscymnus exiguus* Ws., *Exochomus flavipes* Thunb., *Crano-phorus* sp., and one unidentified species; further, 1 nitidulid sp.; 3 chrysopid spp.; 1 coniopterygid sp.; cecidomyiids: *Coccidoplosis* sp., and a species from *Zebediela*; Isometopid: *Letaba bedfordi* Hesse; anthocorid: *Triphleps cocciphagus* Hesse; lygaeid: *Geocoris liolestes* Hesse; pentatomid: *Menida* sp.; mites: one species which is mainly predacious on early grey stage of red scale, and one species which probably feeds mainly on crawlers; fungus: *Fusarium coccophilum* (Desmazières) Wollenweber & Reinking.

We observed that *Anoplolepis* disturbs *A. chrysomphali* which is the most important red scale parasite at Letaba. This ant also disturbed *C. distigma*, *C. wahlbergi*, other coccinellids and spiders.

A flamboyant tree with a 5-foot high crutch, inside the orchard was used to determine the total mileage of ant patrol per tree per day. During 24 consecutive hourly counts, the ants on the trunk were counted in groups of 5, from the ground to the crutch. Every hour we counted the number of ants ascending the trunk during 5 minutes; then the number of ants descending the trunk during 5 minutes. At hourly intervals the speed of a descending and an ascending ant was also determined over the 5-foot high trunk. The average number of ants on this trunk was 72.16. Detailed

calculations, accepted by Bodenheimer, revealed that on a heavily ant-infested tree, i.e. a citrus tree with 1,000 ants on the trunk at one moment, the total ant patrol per day would have amounted to 927,556 miles or 1,492,736 kilometres. But, in order to consider ant patrol from the ants' viewpoint, it is advisable to convert the mileage into smaller units which are more serviceable in the domestic economy of an ant. This is also necessary as the soft scale which the ants tend, as well as the red scale, are sedentary insects. On a heavily ant-infested tree, the ant patrol per day might therefore have amounted to 927,556 miles, or 1,492,736 kilometres, or 4,897,495,680 feet, or 58,769,948,160 inches or 149,273,388,768 centimetres. This explains how effectively *Anoplolepis* protects both red scale and soft scale against their natural enemies, and thus causes epidemics.

In one of the experimental *A. custodiens* plots, after nine months of banding, the commercial value of the citrus crop off 100 banded trees was £83.16.2 i.e. 97.45% higher than the crop off 100 ant-infested trees (Steyn, 1954a).

The second similar red scale-ant correlation project was conducted in 8 plots inhabited by the cosmopolitan brown house ant (*Pheidole megacephala* F.). Two of these plots had Navel trees and six plots had Valencia trees. This project (Steyn, 1954b) similarly incriminated the cosmopolitan *P. megacephala* as the cause of soft scale and red scale outbreaks at Letaba.

It is of practical interest to mention, that, except in heavily infested *Pheidole* plots, very often *Pheidole* only caused defoliation and twig-dieback on a section of a tree, or even only on one or more branches, while with most *Anoplolepis*-infested trees, the whole tree tended to become scaly. Observations showed that the *Aphytis* parasite of red scale, and predacious ladybirds were most active during the daytime. It was thought that the diurnal *Anoplolepis* was, therefore, a greater inhibiting agent against beneficial scale enemies than the nocturnal *Pheidole*.

During the *Pheidole* correlation project, the greatest number of fruit which dropped from a tree because of scale infestations was 212, in comparison with 500 dropped fruit in the case of *Anoplolepis*.

**MIXED ANT POPULATIONS:** The third red scale-ant correlation project revealed that plots which had mixed populations of different ant species, were naturally scale-free (Steyn, 1955). It was thought that many of these natural control plots harboured at least 30 different ant species at Letaba. Both Wheeler (1910) and Bequaert (1922) repeatedly stress Forel's statement that "the most dangerous enemies of ants are always other ants, just as the worst enemies of men are other men".

At Letaba, we observed fights between *Pheidole* and *Anoplolepis*, winter invasions of *Anoplolepis* territories by *Pheidole*, nocturnal captures of *Anoplolepis* nests by *Pheidole*, a diurnal recapture of a nest by *Anoplolepis*, and a fight between *Anoplolepis* and *Cremastogaster* sharing a track on a citrus tree. Fights between *Anoplolepis* and *Polyrachis schistacea* Gerst. were also watched. A tunnel in the outside wall of the insectary was successfully inhabited by *Pheidole*, *Camponotus rufo-glaucus* Jerd. and another ant species during a six-month period.

In the citrus plots with mixed populations consisting of different ant species, proper ant patrol columns were absent from the tree trunks. Often we found no ants on the trunks, or from two to five ants on a trunk at one moment. These ants belonged to two, three, or even five different ant species. It was, therefore, concluded that the different ant species controlled one another.

In two experimental plots it was demonstrated that ant patrol absence in plots with mixed populations of different ant species yielded scale-free trees.

**USEFULNESS OF ANTS:** Letaba findings indicated that both the cosmopolitan *P. megacephala* and *A. custodiens* attack fruit fly (*Ceratitis capitata* Wied.), false codling moth (*Argyroploce leucotreta* Meyr), and boll worm (*Heliothis obsoleta* F.) in citrus orchards. It was, therefore, decided not to eradicate these ants, but to use them on the soil against these citrus pests, and to keep them out of the trees by banding.

**ANT CONTROL:** It was found that discing improved the soil texture and broke up the hard soils necessary for *Anoplolepis* nests.



It was observed that *Anoplolepis* and *Pheidole* populations became very low in previously ant-infested plots which were subsequently planted with daisy lawn (*Lippia* sp.). A vegetal cover was, therefore, recommended.

By increasing the humus content of the soil, ant control was enhanced.

Fifty percent wettable DDT powder was stirred into raw linseed oil to make a sticky paste. This was applied as a 2-inch-wide band just below the tree crutches. This type of band did not kill the ants and also prevented termites from building over it.

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## DISCUSSION

PAUL DEBACH. To what extent have they applied your information in the control of red scale by ant elimination at the Letaba Estates?

J. J. STEYN. When I left, one-third of the Estates was under natural control, and many plots were banded against ants.

PAUL DEBACH. Is the effect of ants on natural enemies greater by predation or by disturbance?

J. J. STEYN. In our experience disturbance of *Aphytis* and ladybirds by ants was apparently more important than predation. We have found dead ladybirds on the cemeteries of *Anoplolepis*. Normally, however, we only noticed ants disturbing the coccinellids. I have not observed active predation on *Aphytis* by ants.

W. L. BROWN, JR. What other important ant species exist and compare with *Anoplolepis custodiens*?

J. J. STEYN. The main important competitors were *Pheidole megacephala* and a *Cremastogaster* species. As mentioned, fights were observed between different ant species, especially *Anoplolepis* and *Pheidole*, as well as *Anoplolepis* and *Polyrachis* species.

T. E. MITTLER. Is there any direct beneficial effect of the ants on the coccids, i.e., do the ants stimulate the coccids to feed and reproduce more rapidly?

PAUL DEBACH. In California, the Argentine ant has no stimulatory effect on the red scale directly. The ant pays no attention to the red scale.

H. A. BESS. One of our graduate students was unable to rear *Coccus viridis* in the laboratory without ants.

R. E. BALCH. Can you explain the difference in barometric pressure on the outer trees?

J. J. STEYN. According to an explanation given me by Mr. Greenbank, Meteorologist at the Forest Biology Laboratory in Fredericton, the higher temperatures adequately explain the lower barometric pressure on the outer trees.

H. A. BESS. Why were the outer two rows of trees in the orchard specially suitable to the ants? Was there an effect from ant populations in the adjacent vegetation?

J. J. STEYN. Higher temperatures, lower relative humidities, and lower barometric pressures made the outer two rows more suitable. Most of the plots had no adjacent vegetation except other plots. On the boundary between the orchard and the veld, when the vegetation was dense, *Pheidole* was encouraged.

M. J. WAY. I should like to confirm Dr. Steyn's point about temperature. In East Africa, *A. custodiens* was most abundant where there were open spaces with poor



ground cover. The ants nested here, taking advantage of the high soil temperatures and not in shaded areas under trees or ground vegetation where soil temperatures were up to 10°C. lower.

P. GARMAN. What effect do ants have on fruit flies in South Africa?

J. J. STEYN. Fruit flies were affected as both *Anoplolepis* and *Pheidole* appeared to prey on the larvae. Fruit flies were very scarce in pure *Anoplolepis* and in pure *Pheidole* plots. At the compost pits and at the packhouse, we repeatedly observed that these two ant species predate fruit fly larvae.

M. J. WAY. With reference to direct benefits of ants to coccids: *Oecophylla luginode* gives benefits to *Saissetia* spp. other than protection from predators and removal of honeydew. Where starvation of the ants is most acute, the coccid population dies most quickly.

J. J. STEYN. In the insectary, we found that some soft scale drowned in their own honeydew when ants were kept away from them.

# The Influence of Other Ant Species on Biological Control of *Oecophylla longinoda* (Latr.)

By M. J. WAY

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## ABSTRACT

Ants are most abundant in tropical rain forest areas where they may have striking effects on the general insect population. This is shown by recent work done in East Africa mainly on Zanzibar Island. Here, large and usually well defined areas are each occupied by one of four mutually antagonistic ant species. Of these, *Oecophylla longinoda* (Latr.) is closely associated with, and greatly benefits, certain honeydew-producing Coccidae. It is also predatory on most other insects, and thus, free living species of Heteroptera, Coleoptera, Hymenoptera and Lepidoptera are scarce in areas which it occupies. *Oecophylla* is particularly important for its control of the coreid, *Pseudotheraptus wayi* (Brown), a serious pest of the coconut palm. The biological control of some insect pests by ants such as *Oecophylla* is remarkably efficient. This is because these ants can maintain large static colonies even when prey is scarce.

Another important ant, *Anoplolepis longipes* (Jerd.), is not usually a predator. However, colonies of *Anoplolepis* were seen spreading into areas occupied by *Oecophylla*, destroying its colonies and replacing it as the dominant ant. A consequence of this was the appearance of many other insect species including *Pseudotheraptus* which caused a big fall in coconut yields. Another consequence was the virtual disappearance of certain Coccidae because *Anoplolepis*, unlike *Oecophylla*, does not protect them from their natural enemies.

Two other important ant species, *A. custodiens* (F.Sm.) and *Pheidole punctulata* (Mayr.), behave like *Anoplolepis longipes*.

The work described in this paper was done in equatorial East Africa, mainly on the island of Zanzibar which has the tropical oceanic climate favourable to insects throughout the year and especially to ants which in numbers and species are more abundant in the tropics than elsewhere in the world. As ants almost invariably have notable effects on other insects they would be expected to have particularly striking effects here.

In Zanzibar and along the neighbouring coastline, large and often well defined areas may be dominated by one of four mutually antagonistic ant species of which the most notable is the arboreal species, *Oecophylla longinoda* (Latr.). In its feeding habits this species follows the common habit of combining hunting with the collection of honeydew from Homoptera but it is exceptional because both aspects are highly developed.

The influence of *O. longinoda* on honeydew-producing Homoptera (Way, 1954b) will not be discussed though it should be emphasized that the association of the ant especially with certain coccids is a very close one and that the coccids which may outnumber the worker ant population by over 4 to 1 provide a continuous supply of honeydew to the ant colony.

Besides tending Homoptera, the large workers of *Oecophylla* are aggressive predators on a wide range of insect species of which the most important is a coreid, *Pseudotheraptus wayi* (Brown). This destroys the female flowers and developing fruits of the coconut palm and can cause virtually 100% crop loss in plantations not inhabited by the ant.

Coconut inflorescences are produced at about monthly intervals throughout the year and provide a constant supply of food to the successive generations of *P. wayi* nymphs and adults. It is noteworthy therefore that, despite this constant danger of attack, a palm can be protected throughout the year by a thriving *O. longinoda* colony even when *P. wayi* is present on adjacent palms. The degree of control is also remarkable because the *P. wayi* population is always small—an average of about 2-3 per

palm. Less than three individuals will cause absolute loss of crop, and thus on trees which it occupies the ant is suppressing a pest whose normal density is too low to be influenced by the conventional predator or parasite. This is because the ant colony can support a large population of predatory workers throughout the year on the dependable supply of food (honeydew) from the coccids with which it is associated. There seems no doubt that primarily predaceous ant species cannot maintain the large static colonies which are needed for efficient biological control, and this is borne out by their behaviour. Those forming large colonies, notably the Dorylinae, are migratory while those that remain static, such as the Ponerinae, can maintain only small colonies on the uncertain food supply.

Where colonies of *O. longinoda* occupy more than about 70% of the palms in a plantation, the *P. wayi* population is so reduced that even uncolonized palms may be undamaged. However, in many areas the ant is replaced by a species of *Anoplolepis*, either *A. longipes*, (Jerd) or *A. custodiens* (F. Sm.). These are ground nesting ants which occupy large, well defined areas from which they were observed spreading amoeba-like into areas occupied by *O. longinoda*. *A. longipes* is not a predator and it tolerates most insects including other ant species except those that show hostility to it. Among the latter is *O. longinoda*, the colonies of which are attacked and destroyed. The tolerant attitude of *A. longipes* to most insects is, however, of significance in biological control for, although it destroys and replaces *O. longinoda*, it allows *P. wayi* and other phytophagous species to attack the coconut palm and cause serious damage.

Another change observed when *A. longipes* replaced *O. longinoda* was the eventual disappearance of the honeydew-producing Coccid species tended by the latter. The *A. longipes* workers solicited the coccids but not assiduously — and thus predator and parasite attacks were seemingly not hindered. Different honeydew-producing species, mainly Pseudococcidae, generally developed in association with *A. longipes*. Not only can these species survive without ant attendance but they can thrive without constant ant attention.

*A. custodiens* and *Phaedole punctulata* (Mayr.) behave like *A. longipes* in destroying *O. longinoda* but tolerating *P. wayi*. There is no doubt that *Anoplolepis* and *Phaedole* species are pests both because they benefit harmful mealy bugs and because they destroy *O. longinoda*. Attempts are being made to control them by promoting vegetative conditions unsuitable for them and also by using insecticides, for they appear to be the only serious hindrance to the extensive spread of *O. longinoda*. Although the coccid species associated with *O. longinoda* must harm some crops such as citrus, coffee and clove, there is no doubt about the benefits which the coconut palm derives from this ant's unique qualities as a predator.

Most of the data on which this paper is based are published elsewhere (Way 1953, 1954a).

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# Effects of Spray Practices on Apple Mites and Their Predators in West Virginia

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## ABSTRACT

Studies in West Virginia apple orchards indicate that *Typhlodromus* mites are the most important predators of phytophagous mites, despite their inherent limitations and extreme scarcity in sprayed orchards. In an abandoned orchard where *Typhlodromus* mites were numerous, European red mite increase was proportional to the destruction of these predators by various pesticides. Infestations remained low and the predators were unharmed on trees receiving seasonal schedules of glyodin and pure ryania, as compared with the opposite situation where standard DDT schedules were applied. However, the predators have increased only slightly and red mites are still numerous in the ryania plots of several commercial orchards where these schedules have been compared for the last three seasons.

Information is also given on the identity, distribution, and biology of *Typhlodromus* mites, and the probable influence of other factors on both phytophagous and predaceous mites is discussed.

An investigation of the causes of increased mite infestation that followed the introduction of DDT in the midforties was started at Kearneysville, West Virginia, in 1952. Although these increases are often attributed to the destruction of natural enemies by DDT and other highly toxic new pesticides, little was known concerning the importance of the beneficial species before the advent of DDT, and still other factors may have been involved.

A comparison of sprayed with unsprayed or abandoned apple orchards revealed wide differences in both phytophagous mite and predator populations. On the abandoned trees predaceous mites of the genus *Typhlodromus* usually outnumbered the phytophagous species and were far more numerous than predaceous thrips, coccinellids, Hemiptera, or Chrysopidae. Populations of the European red mite *Metatetranychus ulmi* (Koch) and the spider mites, *Tetranychus telarius* (L.) and *T. schoenei* McG., remained low with only minor seasonal fluctuations, while those of the clover mite *Bryobia praetiosa* Koch were often rather high early in the season. The opposite situation existed in well-sprayed orchards, where clover mites were extremely scarce and both European red and spider mites were highly destructive. *Stethorus punctum* (Lec.) was the only common predator, and it seldom became effective until mites had reached injurious numbers. There was a rapid transition to former conditions within 3 or 4 years after a sprayed orchard was abandoned.

These observations and the results of earlier studies in Virginia (Clancy & Pollard 1952) suggested the possibility of improving the biological control of orchard mites by substituting relatively nontoxic or selective pesticides for those most destructive to the predators. Since *Typhlodromus* mites seemed more important than other predators, their reaction to various pesticides was determined by spraying small plots in a recently abandoned orchard and making population counts before and at several intervals after treatment. Materials showing selective qualities were then tested in complete seasonal schedules on larger plots in comparison with standard spray programs. Table I shows that, although the *Typhlodromus* mites were highly susceptible to many common pesticides, several materials had little or no effect on them when used at recommended strengths. Those in group 2 are listed in the approximate increasing order of their toxicity, while single applications of any one of the group 3 materials resulted in virtual elimination of the predators.

As noted in a recent paper (Clancy & McAlister 1956), seasonal schedules of ryania plus the fungicide glyodin gave excellent control of the codling moth without

<sup>1</sup> Resigned September 6, 1956.

TABLE I—Toxicity of Pesticides to *Typhlodromus* Mites. Amounts used per 100 Gallons of Water.

Group 1	Group 2	Group 3
Little or No Effect	Partial Reduction of Numbers	Virtual Elimination
Ryania (100% WP), 2-6 lb.	Ryania (96% WP), 4-6 lb.	DDT 50% WP, 2 lb.
Glyodin 34% Liquid, 1-1.5 qt.	Aramite 15% WP, 1.5 lb.	TDE 50% WP, 1-1.5 lb.
Glyodin, 1.5 pt., plus a phenyl mercury compound 7½% Liquid, 6 oz.	Methoxychlor 50% WP, 2-3 lb.	TDE 25% EC, 1 qt.
Captan 50% WP, 2 lb.	Dieldrin 50% WP, 1 lb.	Ovex 50% WP, 1.5 lb.
2,4,5-TP (stop-drop), 0.5 pt.	Lead arsenate, 3 lb., lime, 3 lb.	Flotation sulfur, 10-12 lb.
Aramite 15% WP, 0.5-1 lb.	Ovex 50% WP, 0.75 lb.	Wettable sulfur, 5 lb.
Superior oil, 3 gal. (delayed dormant)	Liquid lime-sulfur, 6 qt.	Bentonite sulfur 30% WP, 6 lb.
Superior oil, 2 gal., dinitro, 1 lb. (delayed dormant)	Ferbam 76% WP, 0.75-1.5 lb.	Parathion 15% WP, 1 lb.
	Dichlone 50% WP, 6-8 oz.	Malathion 25% WP, 2 lb.
	BHC 70% WP, 2 lb.	Malathion 55% EC, 1.5 pt.
	Zineb 65% WP, 2 lb.	EPN 27% WP, 1.5 lb.
	Chlorbenside (Mitox) 20% WP, 1 lb.	Diazinon 25% WP, 3 lb.
	Nicotine sulfate 40%, 1 pt.	Demeton 25% EC, 1 pt.
	Genite 50% EC, 1 qt.	Schradan 90% EC, 8 oz.
	Chlorobenzilate 25% WP, 1 lb.	
	Karathane 25% WP, 0.75 lb.	
	Diazinon 25% WP, 1-2 lb.	



harming the predators, and held phytophagous mites to about the same low levels as those in the check plot. Mite control was attributed to the combined action of *Typhlodromus* predation and the acaricidal effect of glyodin — an advantage not possessed by captan, which is equally harmless to the predators. The addition of lead arsenate to the petal-fall and first-cover sprays for the control of plum curculios and red-banded leaf rollers resulted in a temporary reduction of the *Typhlodromus* mites and slightly higher red mite infestation. On trees receiving standard DDT schedules, however, *Typhlodromus* mites were practically eliminated and heavy red mite infestations developed each summer.

In the abandoned orchard European red mite increase was usually proportional to the destruction of *Typhlodromus* by a wide variety of pesticides that had little effect on the common pest mites. Appreciable infestations never developed in this orchard unless the *Typhlodromus* mites were seriously reduced by the application of harmful pesticides. *Leptothrips mali* (Fitch) was the only other predator abundant enough to be of any importance on the unsprayed trees.

The glyodin-ryania schedule is also being compared with standard DDT schedules in larger plots of several commercial orchards where all sprays are applied by the growers. However, the routine use of acaricides with the DDT schedules but not with ryania has usually allowed heavier mite infestations to develop in the ryania plots and thus prevented a direct comparison between the two materials. *Stethorus punctum* became most abundant on the trees with the heaviest mite infestations, regardless of spray schedules, but *Typhlodromus* mites seldom appeared except in the ryania plots from about midsummer onward. These mites became most numerous in August and September, when they sometimes outnumbered European red mites in one of these orchards, indicating effective biological control as compared with increased mite infestation in the adjoining DDT-sprayed plot. In the other commercial ryania plots the *Typhlodromus* mites occurred in smaller numbers with little evidence of control thus far, though some increase was noted in 1956. Very few other predators have been found in any of these orchards.

Although predation has shown only limited improvement in the commercial orchards during the last three seasons, more time may be required to determine the final outcome.

Collections of *Typhlodromus* mites from apple foliage revealed a complex consisting of *pomi* (Parrott), *fallacis* (Garman), and two slightly different forms near *fallacis* which may be *umbraticus* Chant and a variety of *cucumeris* (Oud.). Those of the *fallacis* group were most abundant and widespread. The same species were also collected from many native trees, shrubs, and weeds together with *conspicuus* (Garman) and an undescribed form. *T. cucumeris* (Oud.) and *marinus* (Will.) occurred only in winter collections of surface debris in the abandoned orchard.

A greater variety of predaceous and saprophytic mites were collected from apple bark, surface debris, and soil beneath the abandoned trees, but these rarely if ever occur on the foliage.

Several workers have found that many *Typhlodromus* mites prefer Eriophyidae and *Tetranychus* spp. as prey, feeding very little if at all on *Bryobia* and to a rather limited extent on the European red mite. The abundance of *Typhlodromus* spp. and *Bryobia* in contrast to the scarcity of other Tetranychidae on unsprayed trees in West Virginia also suggests that these predators must have other food sources.

We are finding large numbers of apple rust mites *Vasates schlectendali* (Nal.) in the abandoned orchard early in the season, and the body contents of many *Typhlodromus* mites are then of the same light tan color as the eriophyids. It has been noted that *Typhlodromus* increases most rapidly at this time and that reproduction declines after midsummer as rust mites become less numerous. In the commercial-orchard ryania plots, however, both eriophyids and *Typhlodromus* are more abundant during late summer, the predaceous mites usually attaining higher populations in those plots having the most rust mites. Although *Typhlodromus* seems to prefer the eriophyids, it will feed readily on European red mites when rust mites are scarce.

Another possible food source is suggested by the recent findings of D. A. Chant in England on the phytophagous habits of apple *Typhlodromus* mites, including their ability to reproduce and develop on various plant proteins in the absence of animal food. This may help to explain the remarkable persistence of these mites during late summer on leaves practically devoid of known prey, and could greatly increase their chance of survival during periods of phytophagous mite scarcity.

In autumn female *Typhlodromus* mites move to the twigs and branches, where they seek protection for the winter. A few are carried to the ground on falling leaves, and others crawl under loose bark, but only those finding deep crevices, especially in the ends of broken twigs and around old scars, are able to survive. Colonies of from 2 or 3 to a maximum of 65 mites were found in these locations in March, though many similar places were devoid of predators or had only dead specimens. Winter mortality probably accounts for most of the great annual reduction in populations on leaves between autumn and spring, and may seriously limit the utilization of *Typhlodromus* spp. in the biological control of orchard mites. Even on unsprayed trees they seldom become numerous until June, when red mites have already completed two or three generations.

When overwintering *Typhlodromus* mites were brought into the laboratory and supplied with *Tetranychus telarius* on bean leaves, they began feeding within a day or two and ovipositing in about a week. Those confined to bean leaves without prey did not lay eggs or live as long. Ballard (1954) reports similar results with *Typhlodromus fallacis*, which also fed on larvae of the European red mite.

Red mites are more generally distributed over the leaves than are *Typhlodromus* mites, which congregate mainly along the midribs and larger veins on the undersides of the leaves. However, the predators are very active and move about freely in search of food, depositing their eggs largely at random over the lower leaf surface, fastening most of them to the tips of leaf hairs. There was little difference in the relative abundance of red mites and *Typhlodromus* spp. on leaves of various ages throughout the season.

Attempts to determine the reasons for outbreaks of orchard mites following the change-over to DDT have been seriously hampered by the lack of previous data on the mites and predators, and by the absence of lead arsenate-sprayed orchards that could be used in such a study. Although the predator explanation is widely accepted, both lead arsenate and the sulfur fungicides are destructive to the predaceous mites (Table I), and it is doubtful that they could have survived the former spray programs in much larger numbers than they can those in current use. In fact, the predaceous mites were nearly eliminated and a severe red mite infestation developed on trees in the abandoned orchard sprayed with the old sulfur-bordeaux-lead arsenate schedule. The addition of DDT to the same schedule in another plot resulted in about one-third more red mites and even fewer *Typhlodromus* mites. Since insect predators are relatively scarce, even in isolated abandoned orchards that have not been sprayed for many years, it is doubtful that they were ever capable of economic mite control.

In a similar study on pears in California, Huffaker & Spitzer (1950) concluded that red mite increase under the DDT program was due largely to the omission of summer oils that were used as stickers with lead arsenate. Since the oils are effective acaricides and were also used with codling moth insecticides in most eastern apple orchards, this explanation is highly plausible.

Several workers (Fleschner 1952, Hueck 1953, Huffaker & Spitzer 1950) have shown that DDT may favor mite increase independently of other factors, though its mode of action is uncertain and the results obtained were often quite variable. The influence of plant nutrients on mite reproduction is well known, and the ability of plants to absorb and translocate DDT (Fleschner 1952, Huffaker 1948) suggests the likelihood of a similar relationship. We were unable to establish a positive relation between mite increase and DDT, apart from its effect on the predators, despite some indication of its presence. On the other hand, in the commercial-orchard ryania plots where DDT has not been used for the last 2 to 5 years, there has been no marked decline in red mite infestation except that caused by *Typhlodromus* predation in one of these orchards.

The great improvement in foliage condition and vigor that has followed the use of modern spray and fertilization programs may also be conducive to heavier infestations, as mites are known to prefer more vigorous host plants.

It is concluded, therefore, that mite outbreaks are probably due to a combination of these factors rather than to any single cause, and the relative importance of each factor will naturally vary according to local circumstances. Apparently certain repressive factors have been replaced with others that favor mite infestation.

The increasing complexity of apple spray programs obviously decreases the possibility of biological control unless we can reverse the present trend by devising programs based on materials that are relatively harmless to the more important natural enemies. Considerable progress has already been made along these lines in Nova Scotia (Pickett 1955) and England (Massee 1954), where insect predators are more numerous and mites have ceased to be a problem except in orchards sprayed with DDT and other toxic pesticides. It now remains to be seen whether this approach will succeed under different conditions in other fruit-growing areas.

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# Some Observations on the Effect of Insecticides and Acaricides on the Population of the European Red Spider Mite (*Metatetranychus ulmi* Koch) and its Principal Predators in Commercial Orchards in the Netherlands

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## ABSTRACT

During the last 3 years observations on the effects of insecticides and acaricides on the population development of predatory insects and mites have been made. From these it appears that ovo-larvaecides, either alone or in combination with DDT, caused a sharp decline in red spider density followed by a similar decline in predatory insects which are dependent on the numbers of prey. Predatory mites, however, were scarcely affected.

Application of the ovo-larvaecides together with parathion resulted in a very good control of the red spider mite, but also in an almost total destruction of the predatory mites and bugs.

On untreated trees, the red spider reached such a high density early in the season that damage occurred despite the presence of predators. Later, the pest declined because of lack of food caused by severe bronzing of the leaves. At the same time the predatory insects declined in numbers, but the predatory mites were scarcely affected.

Recommendations are made to those who wish to combine biological and chemical control under Dutch conditions.

## INTRODUCTION

The European fruittree red spider mite has become one of the major pests in the apple growing areas in the Netherlands during the last 30 years. In this period remarkable changes in cultural practices have taken place. From these the introduction of new apple varieties which often are more susceptible to red spider mite attack, the introduction of new rootstocks and allied spacings and form of the tree, the increased soil management and use of fertilizers, the totally different control measures against the various fruittree pests are mentioned here.

On one hand these changes did increase the amount and the quality of suitable food for the European red spider mite; on the other hand the application of spray chemicals did not only affect the European red spider mite but also its predators.

During the last three years some observations have been made on the effect of the application of phosphorous insecticides, viz parathion, malathion, TEP<sup>1</sup>) and EPN 300<sup>2</sup>, and acaricides viz the ovo-larvaecides, ovotran (PCPCBS<sup>3</sup>), chlorbenside<sup>4</sup> and Tedion, either alone or in combination with parathion or DDT, on the fruittree red spider mites and their predators viz Typhlodromus mites (Collyer, 1956, Dosse, 1953, Kuenen, 1947, Masee, 1954 a.o.) and some bugs.

## METHODS

The observations and trials were carried out in commercial orchards. Spraying was done with an ordinary spraying machine as a preblossom spray and/or as a spray shortly after blossom time (apple sawfly spray time). Population counts on treated and untreated (check) trees were made by counting weekly the numbers of mites, eggs and predators present on samples of 100 leaves.

As the predatory Typhlodromus mites and the bugs *Anthocoris nemorum* L. and *Orius minutus* L. were the most important predators present, only the figures of these predators are given here (*T. vitis* Oud., *T. tiliae* Oud., and *T. tiliarum* Oud. were present; they were however not separately counted).

In the trial plots only the fungicides tetramethyl thiuram disulphide (TMTD), zinccarbamate or organo-mercury sprays, which are known to have little or no effect

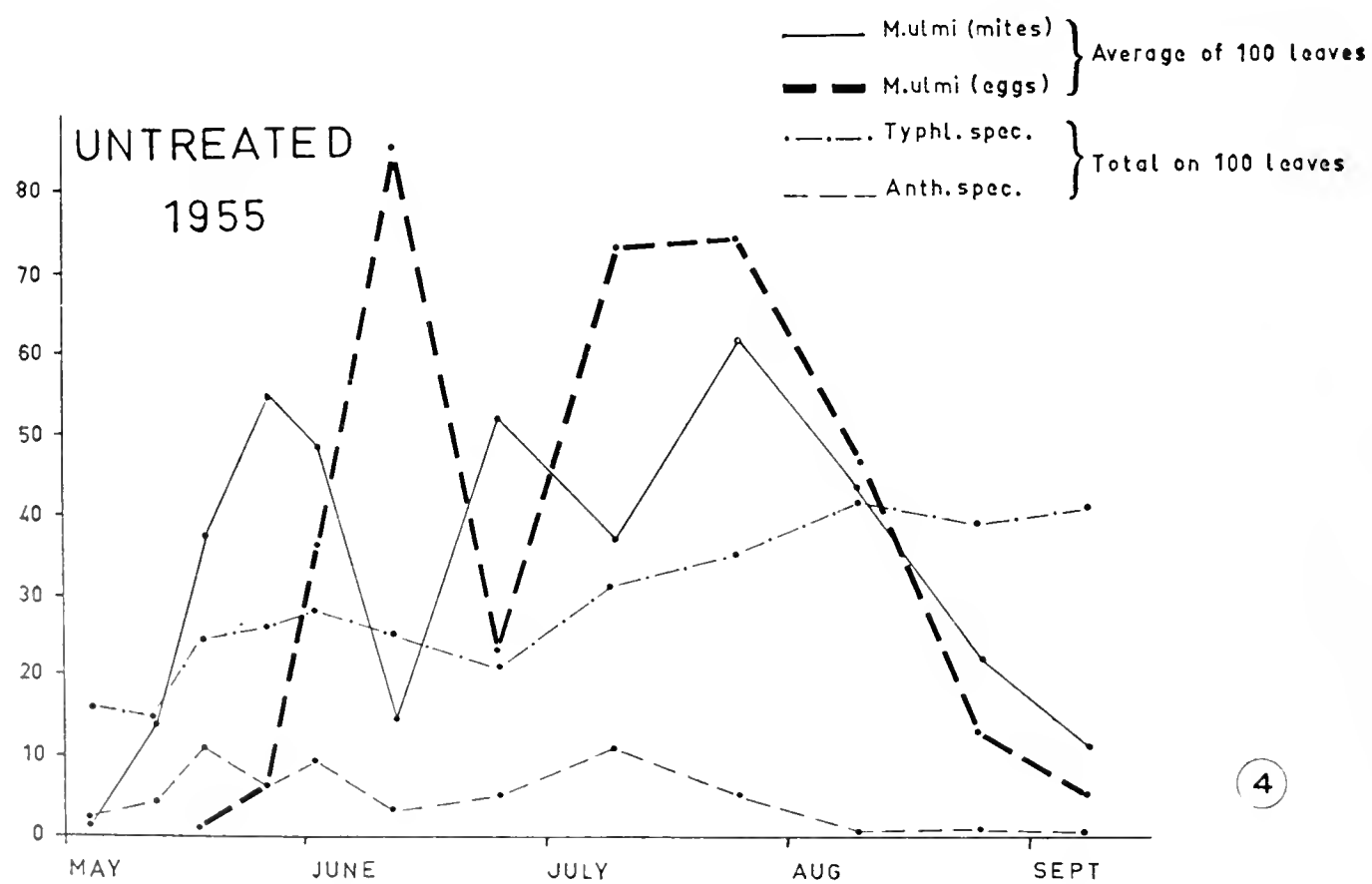
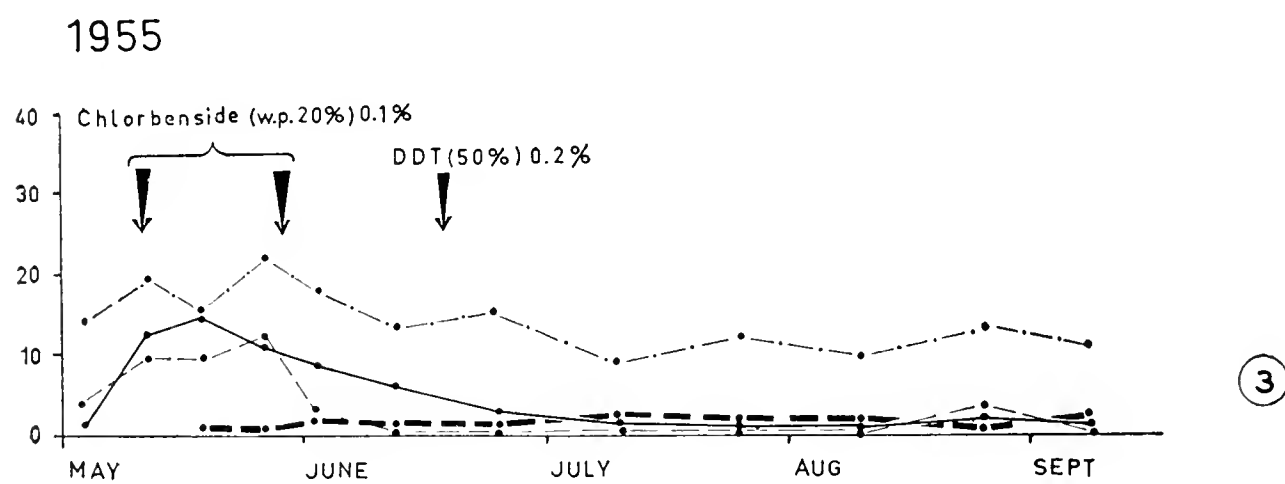
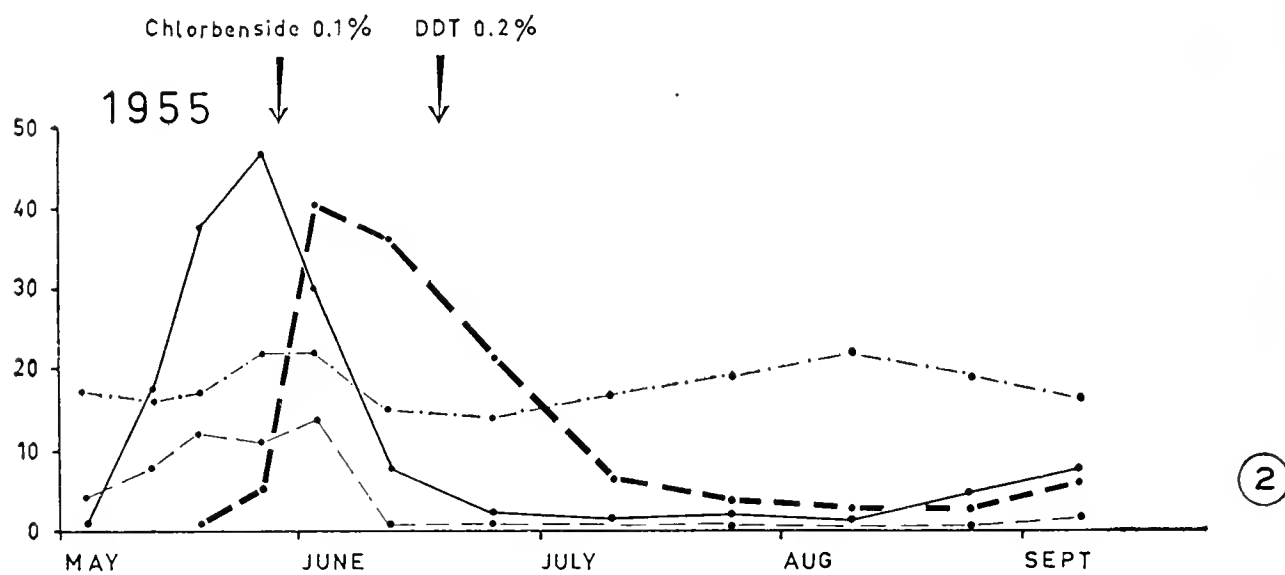
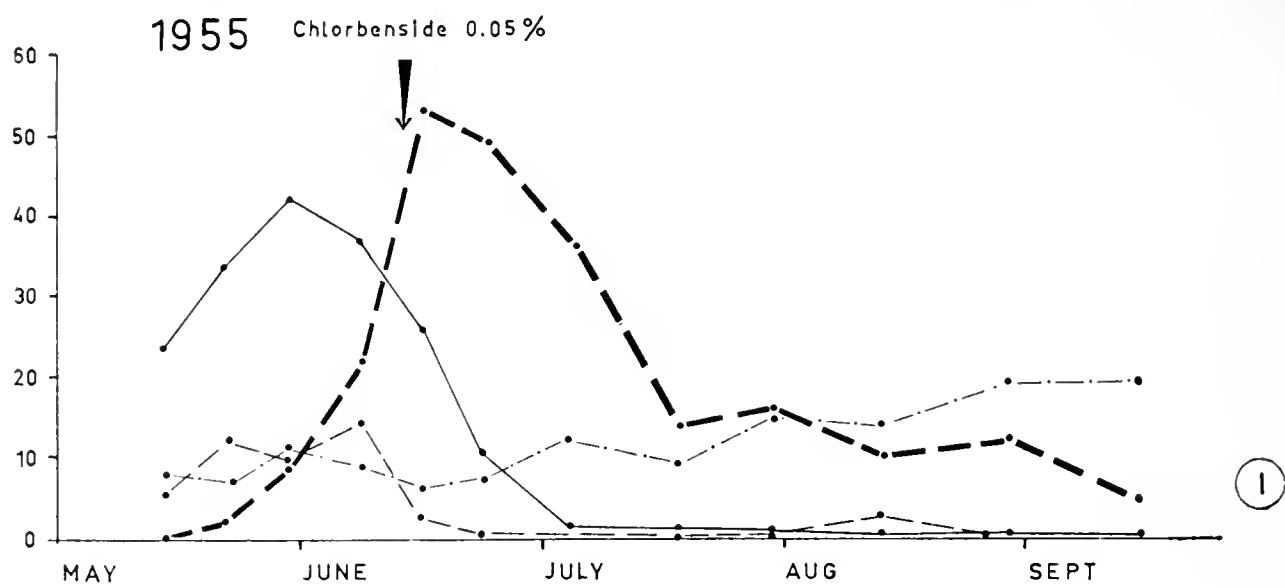
<sup>1</sup> Tetraethyl pyrophosphate.

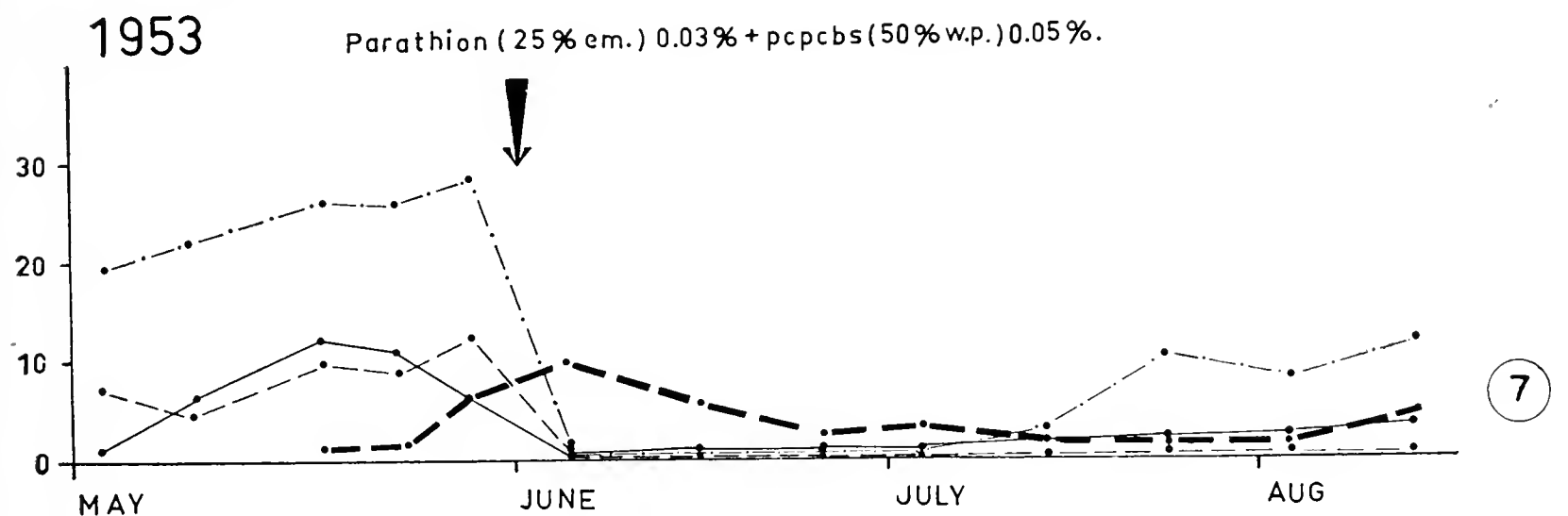
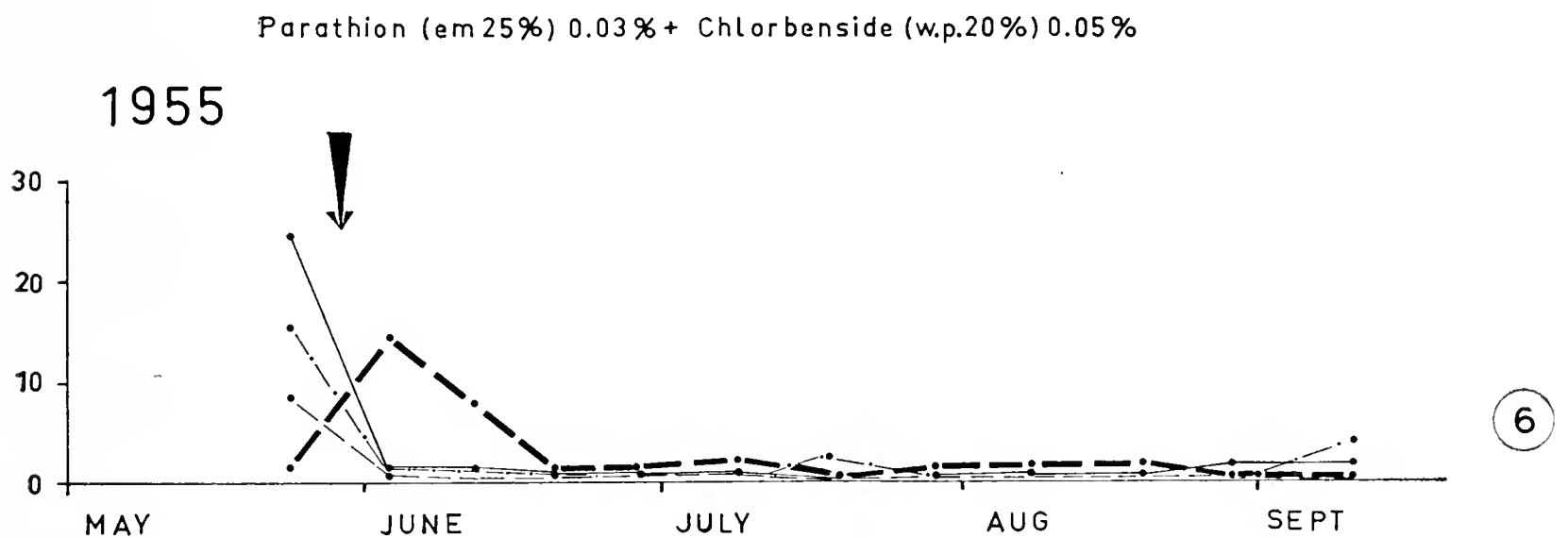
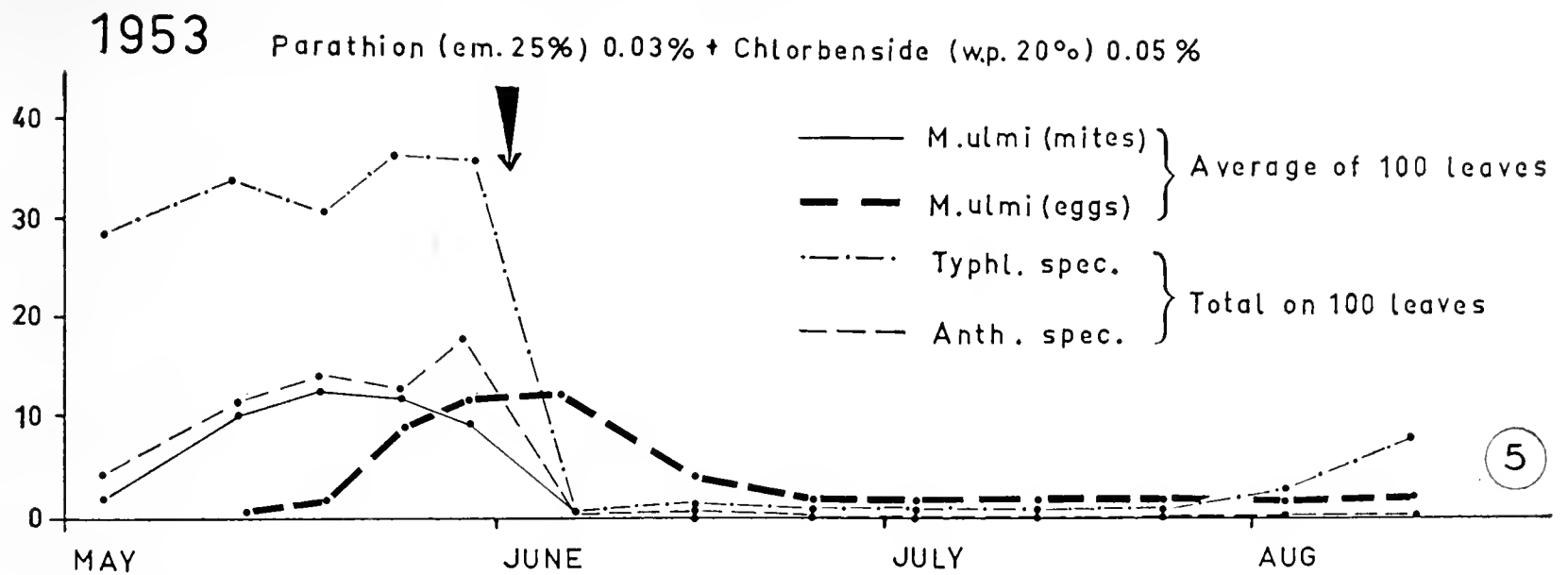
<sup>2</sup> Aethylparanitrophenylthionobenzenefosfonate.

<sup>3</sup> Parachlorophenyl parachlorobenzenesulfonate.

<sup>4</sup> p-chlorobenzyl-p-chlorophenylsulphide.







on the red spider mite populations, were applied; these fungicides were also applied in the "untreated" plots.

The experiments were started in commercial orchards in which in the previous year a normal routine spraying schedule with fungicides and insecticides had been carried out.

This is the reason why the populations of the predators of the red spider mite are small in comparison with the populations in untreated orchards. In untreated orchards, however, the populations of the red spider mite in general are much smaller than in well kept orchards. The reason for this phenomenon is not yet known.

## RESULTS

From the experiments it appeared that:

1. Application of the ovo-larvaecide chlorbenside either alone or in combination with DDT<sup>5</sup> (used for the control of the fruittree leafroller and the codling moth)

<sup>5</sup>w.p. 50%, 0.2%.

resulted in a decline of the spider mite population (eggs and mites) followed by a decline of the population of predatory bugs, being dependent on the numbers of mites present. The populations of the *Typhlodromus* mites, however, were hardly affected. In most cases they were present in pretty large numbers, even in those cases where only a few red spider mites or eggs were left (see Graphs 1-4).

2. Application of the ovo-larvaecides together with parathion resulted in a very good control of the red spider mite, but also in an almost total destruction of the predatory mites and bugs (see Graphs 5-7).

3. On the untreated trees of the 1955 trials the red spider mite population already early in the season reached such a high level that discoloration of the leaves occurred notwithstanding the presence of predatory mites and bugs. Later in the year the red spider mite population decreased in number by lack of food resulting from the severe bronzing of the leaves. At the same time the population of the predatory bugs decreased but the population of the *Typhlodromus* mites was hardly affected (see Graph 4).

### GENERAL DISCUSSION

The most important problem still is: does a quantitative relation exist between mites and predators and if so, is in those cases where a negative correlation occurs, this correlation based on the activity or inactivity of a certain number of predators?

Graph 4 shows the populations of both predators and spider mites present in the "untreated" plots. In interpreting these figures we must bear in mind that in the year before in these plots a normal routine spray schedule was carried out. These treatments had without any doubt an effect on the number of red spider mites and predators present in spring. In these "untreated" plots, however, already early in the season the red spider mite population reached such a high level that discoloration of the leaves occurred.

The effect of the use of organo-phosphorous compounds appeared to be extremely destructive with regard to the predator population.

The effect of the ovo-larvaecides on the *Typhlodromus* population, however, was hardly visible.

Those who intend to combine biological and chemical control of the red spider mite are suggested to apply these ovo-larvaecides a.o. PCPCBS and chlorbenside.

We in the Netherlands, however, can't yet drop the organo-phosphorous compounds from our chemical spray schedule as they are excellent insecticides to control the green apple aphid (*Aphis pomi* de G.), the codling moth (*Enarmonia pomonella* L.) and the fruittree leafroller (*Adoxophyes reticulana* Hb.) which are also serious pests in our orchards.

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# The Control of Phytophagous Mites in Swiss Vineyards by *Typhlodromus* Species

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## ABSTRACT

Since 1953 the problem of the red spider on the vine has been studied at Nyon. The results of these investigations show that the most prevalent species of the red spider is identical with *Metatetranychus ulmi* (Koch). The useful fauna observed on fruit trees (bugs, thrips, coccinellids, Hemerobiidae) is not very active in the vineyard. On the other hand predatory mites of the genus *Typhlodromus* appear to be an effective factor limiting populations of *M. ulmi*. The most common species are *T. tiliae* Oudemans and *T. aberrans* Oudemans.

The effectiveness of these predators is at its highest point when *M. ulmi* eggs are hatching and its destructive work is concentrated on very small areas as the buds are not yet developed, or just so. During this time the death rate of *M. ulmi* due to *Typhlodromus* varies from 13-100%. In summer, the severity of the attack by *M. ulmi* is closely related to the presence of *Typhlodromus*. There are few predators other than mites: a few thrips and a bug, *Anthocoris nemorum* L.

It has been noticed that there is a close relation between the level of *Typhlodromus* population and the kind of spraying program followed by the vine grower. Laboratory tests on vine leaves with *Typhlodromus* (especially *T. tiliae*) show that parathion, systox, zineb (zinc ethylene bis dithiocarbamate) sulphur dust and lime sulphur are definitely toxic to *Typhlodromus*. Bordeaux mixture, Captan, copper oxychloride, wettable sulphur and Nirozan (tetranitrocarbazol) do not affect the populations of this predator. DDT seems to be moderately toxic and takes an intermediate position between these two groups.

Since 1950 the vine-growers of Switzerland have become more and more concerned by an increase in the severity of mite damage in their vineyards. In some cases severe infestation of the young shoots in the spring retards the development of foliage and distorts the leaves and flowers. In other cases, summer infestations discolour the leaves causing them to appear a dull, greyish colour like lead, and the normal maturation of the wood is prevented. Since 1953 the writer has been investigating the problem of the mites on vines with two aims; firstly, to discover what species cause the damage which is observed, and secondly, to study the complex of predators or parasites which could be useful as controlling agents of phytophagous mites. The lack of precise information in the literature necessitates a long term study.

Investigations have shown to date that the most prevalent species of red spider on vines is morphologically identical with *Metatetranychus ulmi* (Koch), a species which is also a serious pest of fruit trees. The larvae of the generation which hibernates as eggs on the vine stocks hatch about the 20th of April. During the summer there are from four to five generations which overlap so that eggs as well as adults and nymphs can be observed at almost anytime.

The potential for increase of the population is enormous. A study of the factors limiting this increase has shown that the red spider under natural conditions is partially controlled at least not only by abiotic factors but also by biotic ones. Observations made over three years confirm that much of the useful fauna observed on fruit trees (e.g. Hemiptera, thrips, coccinellids, and Hemerobiidae) is not abundant in the vineyard. On the other hand, predatory mites of the genus *Typhlodromus* Scheuten are present in all Swiss vine-growing districts, and they appear to be a much more effective factor limiting the abundance of *M. ulmi*. The most common species of this genus is *Typhlodromus tiliae* Oudemans, and sometimes *T. aberrans* Oudemans also occurs. Both of these species feed both on mites and on the contents of leaf cells; they are facultative predators.

The voracity of *Typhlodromus* is surprising and they eat eggs as well as nymphs and adults. *T. tiliae* starts activity before the hatching of *M. ulmi* in the spring; its temperature threshold of active searching for prey is about 10 degrees C. Therefore, this predatory mite has no complete hibernal dormancy; whenever the winter temperature is mild, the mite emerges from its overwintering site under bark and starts searching for food. The eggs of *M. ulmi* are then an easy prey and occasionally the predator will eat even the larvae of coccids. When *M. ulmi* hatches in the spring the typhlodromids feed extensively on the young larvae. This great voracity seems partly due to the lack of leaves at this time which may supplement the diet of this predator, and to the long period of fasting which occurred during the cold spell. The effectiveness of this predator is thus at its highest point when *M. ulmi* eggs are hatching. Contributing to this is the fact that its destructive work is concentrated on a very small area as the vine buds are not yet completely developed. Table I gives an idea of this predatory activity; counts were made on 500 leaves but from this data only 20 leaves are shown here. The death rate of *M. ulmi* varies from 13 to 100 per cent with the mean value at 60 per cent. At this stage of leaf development the typhlodromids go from one leaf to another, whereas later they tend to remain on one leaf over which they wander at regular intervals. The typhlodromids are found at the base of the main veins on the underside of a vine leaf.

TABLE I — Mortality of *M. ulmi* due Essentially to *Typhlodromus* (mainly *T. tiliae*) on Vine Leaves just after Hatching (13.5.55.).

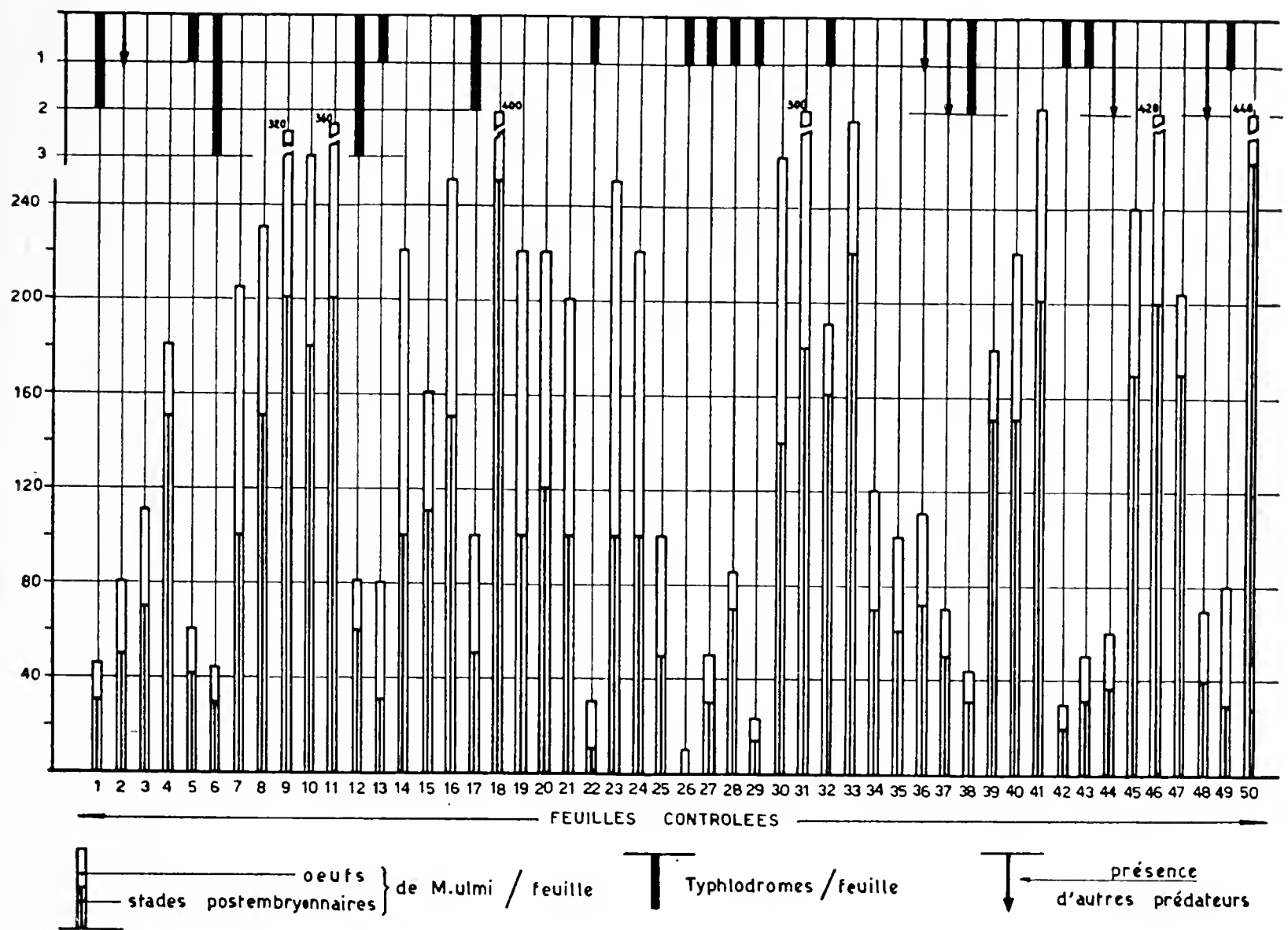
Leaves	<i>T. tiliae</i>	<i>M. ulmi</i>		
		living	larvae and adults dead	mortality rate %
1	1	70	29	29
2	1	42	10	19
3	0	27	4	13
4	1	5	10	66
5	0	5	10	66
6	0	10	10	50
7	4	1	15	94
8	6	0	23	100
9	7	0	3	100
10	2	3	18	86
11	4	4	25	86
12	5	17	20	54
13	3	6	15	71
14	3	20	15	43
15	2	8	10	55
16	1	6	17	74
17	1	19	5	21
18	4	6	24	80
19	4	21	28	57
20	5	23	35	60

Table II shows the distribution of *Typhlodromus* in summer. The leaves of vine considered here were taken from three plants only but it can be seen that on these leaves the severity of attack by *M. ulmi* is closely related to the presence of *Typhlodromus*. Only a few predators other than mites occurred and these were thrips and a bug, *Anthocoris nemorum* L. The low level of *Typhlodromus* population, due in this instance to parathion spraying, did not permit a good biotic control of the red spider owing to the continuous reinfestation from leaves which had no *Typhlodromus*; the predator was prevented from maintaining control on the few leaves inhabited.

It has been noticed several times in vineyards that there is a close relation between the level of *Typhlodromus* population and the spray programme followed by the vine-grower. Laboratory tests have demonstrated the effects of various chemicals on *T. tiliae*



TABLE II — Relation between *M. ulmi* and *Typhlodromus* (mainly *T. tiliae* with a few *T. aberrans*) in a Severely Infested Vineyard.



and these results are shown in Table III. This shows that parathion, systox, zineb, sulphur dust, and lime sulphur are decidedly toxic to *Typhlodromus*. On the other hand, Bordeaux mixture, captan, copper oxychloride, wettable sulphur, and nirosan do not materially affect this predator. DDT is moderately toxic and occupies a position intermediate between these two groups.

TABLE III — Laboratory Test on Vine Leaves with *Typhlodromus* (esp. *T. tiliae*).

Product	Active matter	Number of <i>Typhlodromus</i>	% Mortality rate after	
			2 hr.	20 hr.
Control		46	0	5
Parathion	20 g	35	100	—
Systox	20 g	28	100	—
Zineb*	250 g	34	75	100
Sulphur dust	100 %	27	70	75
Lime sulphur (32° Be)	450 g	37	59	62
DDT	100 g	39	22	60
Nirosan**	250 g	30	37	31
Wettable Sulphur	225 g	30	18	17
Copper oxychloride	375 g	32	0	9
Captan	125 g	26	1	8
Bordeaux mixture	500 g	36	3	7

\*Zineb = zinc ethylene bis dithiocarbamate

\*\*Nirosan = tetranitrocarbazol

The occurrence of *Typhlodromus* is not confined to the vineyards of the French part of Switzerland; it has been recorded in the other parts of this country as well. In France, this predator appears to play an important role in the control of red spider

populations, especially in Southern France near Montpellier and Beaucaire, where as many as 30 *T. aberrans* per leaf have been observed exhibiting great activity.

What practical conclusions can be drawn from these facts for the control of the red spider on vines with regard to the spray programme? It is suggested that the vine grower must take full advantage of the valuable help these predators can afford to him, and be careful to restore the faunistic balance which has now almost everywhere been destroyed at the expense of *Typhlodromus*. This desirable situation will be attained only by steps and after several years. It will be difficult to find a satisfactory compromise between chemical pest control and the protection of useful fauna in viticulture. However, there are now available a few products, insecticides and fungicides, which permit this ideal solution of good crop protection at a low cost.

#### DISCUSSION

A. M. MASSEE. Does Bordeaux mixture destroy populations of typhlodromid mites?

D. A. CHANT. Apparently not.

A. M. MASSEE. Why are predacious insects largely absent from vineyards in Switzerland?

D. A. CHANT. Predacious insects are probably absent from Swiss vineyards because of their habit of overwintering on the woody parts of plants. These parts are largely removed each autumn from the vines, a normal cultural practice.

P. GARMAN. Have you had any evidence of resistance of *Typhlodromus* to insecticides?

N. H. ANDERSON. Yes. In British Columbia it has been found that three applications of parathion per year for three years have produced a strain of *Typhlodromus occidentalis* Nesbitt that is resistant, or tolerant, to this chemical.

# Influence of Treatments on Predators and Other Limiting Factors of *Metatetranychus ulmi* (Koch)

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## ABSTRACT

*The application of insecticides is perhaps the most spectacular method of upsetting numerical regulation of arthropods on cultivated crops. It is, however, by no means the only influence with this result, and three others are to be considered.*

1. *The destruction of predators is generally supposed to be the main factor contributing to outbreaks of red spider following the use of certain insecticides. When outbreaks occur, generally predators are absent. Absence of predators, however, is not always followed by an outbreak and the quantitative relation between mites and their predators has not been investigated with sufficient accuracy to prove that the negative correlation is based on a cause-effect relationship.*

2. *When trees are sprayed, many phytophagous arthropods are killed. This reduces competition and red spider which may remain can increase much more vigorously than before. Though competition is difficult to measure, it can be shown to exist by means of studying the abundance of mites of different species found on small apple trees.*

3. *Fertilizers induce better growth of trees, and the chemical composition of leaves may be altered by their use. No correlation between magnesium, potassium or phosphorus content on leaves and mite abundance could be found, but a high nitrogen content is correlated with high numbers of red spider. Of course, this may not be a casual correlation.*

4. *Low concentrations of DDT have been shown to increase the numbers of eggs produced by adult female red spider.*

*The conclusion reached is that not only the destruction of predators but also other factors help to create the "red spider problem", and the general ecology of the tree should be studied more thoroughly.*

## INTRODUCTION

We have, by now, sufficient evidence that certain insecticidal treatments can provoke outbreaks of certain mites and insects. What needs to be studied is the exact mechanism of influence of the different factors of general orchard treatment on the arthropod fauna living on the trees.

A plant growing in nature generally serves as food for a number of arthropods. The arthropods again are, to some extent, eaten by predators or by parasites.

The varying magnitude of birth-rate and death-rate depends on climate, food, predators, population-density and interference of other non-predacious species.

This is also true for arthropods of economic importance living on cultivated plants and when these are being studied we must consider all ecological factors which can have a measurable influence on birth-rate and death-rate.

We have been studying a number of these factors for some time now in Holland, and although no definite results have been obtained, it seems to be worth while to draw attention to some of our results.

We shall discuss four points.

KILLING OF THE PREDATORS

Although ecologists in general are very much in doubt about the effect of predation on population-density, economic entomologists assume this to be the case on too restricted evidence without further proviso. They generally believe that predators control the population-density of phytophagous arthropods, and therefore that their destruction will induce an outbreak. In many cases it has been proved that indeed this relation existed, but unless it is actually proved beyond doubt we cannot be sure it is true. Only recently some evidence has been put forward showing that *Metatetranychus ulmi* (Koch) can be actually controlled by predators.

But, on the other hand, in some cases we get no increase of red spider in spite of the destruction of the predators. In those cases other factors apparently hold the mites in check and it would be interesting to know what kind of factors these are.

The following data show a case where destruction of predators gave no immediate increase of *M. ulmi*.

TABLE I — Mites: Total Numbers Found on 8 Samples of 100 Leaves, taken in the Course of the Year. Hemiptera: Number Found by Tapping, also Total from all Collections During the Year.

		apple; var. Goudreinette				apple; var. Bellefleur			
		unsprayed plots		sprayed plots		unsprayed plots		sprayed plots	
<i>M. ulmi</i>	1953	6				154			
	1954	4	43	15	21	95	235	19	60
	1955	84	519	3739	9878	318	1702	3691	24055
<i>Typhlodromus</i> spp.	1953	130				113			
	1954	415	379	1	0	275	219	1	1
	1955	403	666	0	2	258	442	0	1
Predacious Hemiptera	1953	137				86			
	1954	411	556	41	7	293	371	9	12
	1955	420	276	8	5	338	84	2	1

In another case we got the following results after one season's treatment.

TABLE II — Numbers of Mites and Hemiptera as in Table I.

	O	P	P + F	F
<i>M. ulmi</i>	281	940	520	1314
<i>Typhlodromids</i>	60	2	0	10
<i>Hemiptera</i>	126	33	40	137
<i>Brvobia</i> sp.	396	25	8	472
<i>Schizotetranychus</i> sp.	591	24	6	198
<i>B. oudemansi</i>	18	22	17	1

O=untreated, P=parathion, F=fungicide.

It should be added that we, like many others, have found a number of cases where the disappearance of the predators coincided with the beginning of the increase of *M. ulmi*.

COMPETITION

Although the term competition is rejected by some ecologists in a number of cases in which it has hitherto been used, I think it can be applied in the case when a limited amount of food is used by different species.

Now there are many phytophagous arthropods on apple trees, and it is worth considering whether their destruction by insecticides reduces their competitive value to such an extent that the remaining species profit from their absence through an increase in the amount of available food.

In Holland considerable numbers of mites of the species *Bryobia praetiosa* Koch, (*B. rubrioculus*), *Schizotetranychus* spec. and *Brevipalpus oudemansi* (= *Tenuipalpus oudemansi*), may be found in neglected orchards and they are easily killed by many insecticidal sprays.

This is clear from the following data:

TABLE III—Destruction by Insecticides (and Fungicides) of Mites other than *M. ulmi*. Numbers as in Table I.

		apple; var. Goudreinette				apple; var. Bellefleur			
		unsprayed plots		sprayed plots		unsprayed plots		sprayed plots	
<i>B. praetiosa</i>	1953		1125				1078		
	1954	6119	10072	167	16	1569	3330	13	9
	1955	2838	3478	46	0	673	357	10	0
<i>Schizotetra- nychus</i> sp.	1953		—				—		
	1954	107	107	4	0	1726	438	3	20
	1955	550	154	9	0	1354	66	3	5
<i>T. oudemansi</i>	1953		—				—		
	1954	985	448	2	5	680	351	0	1
	1955	568	919	0	0	353	232	0	0

Now we have further been able to show that there is competition on the leaves. On a number of two-year-old apple trees, planted under glass, the numbers of mites were counted on ten leaves of each tree at irregular intervals during the summer.

The results show that the presence of *Bryobia* inhibits the growth of the *M. ulmi* population, while *M. ulmi* also reduces the numbers of *Bryobia* developing (Fig. 1). When one species is alone it attains much higher numbers than when the other species is present. The influence of *Bryobia* on *M. ulmi* may be less pronounced than the influence of *M. ulmi* on *Bryobia*.

It therefore seems quite possible that reduced competition is a factor which has some significance in the outbreaks of *M. ulmi* on sprayed apple-trees.

FOOD

In population dynamics the quantity and quality of food play an important part. Apart from spraying, cultural treatments of trees include fertilizing and pruning. This has a great influence on growth and production of the tree and it is obvious that phytophagous arthropods are affected to some extent too, by this change of food.

Aphids, preferring young and succulent shoots show enormous development on vigorously growing trees; *Eriosoma lanigerum* does the same, specially on the shoots coming from dormant buds on the thicker branches inside the tree crown.

Quantitative data are lacking, but we have observed an enormous increase of *Eriosoma* on trees which were pruned and to which fertilizers were applied, but which were not sprayed.

The increase in quantity and quality of food for mites is much less obvious, but may, nevertheless, be of importance. For this reason a great number of analyses were made of leaves from different orchards, well-kept and neglected.

There could not be found any correlation between Mg, K or P and the numbers of mites, but with N<sub>2</sub>, there were some interesting differences which are shown in Fig. 2.

This shows that there is a correlation, which may be a question of cause and effect. But we should remember that in practice spraying and the application of fertilizer show a very strong positive correlation. It is not certain, therefore, that fertilizing causes a higher population of mites.

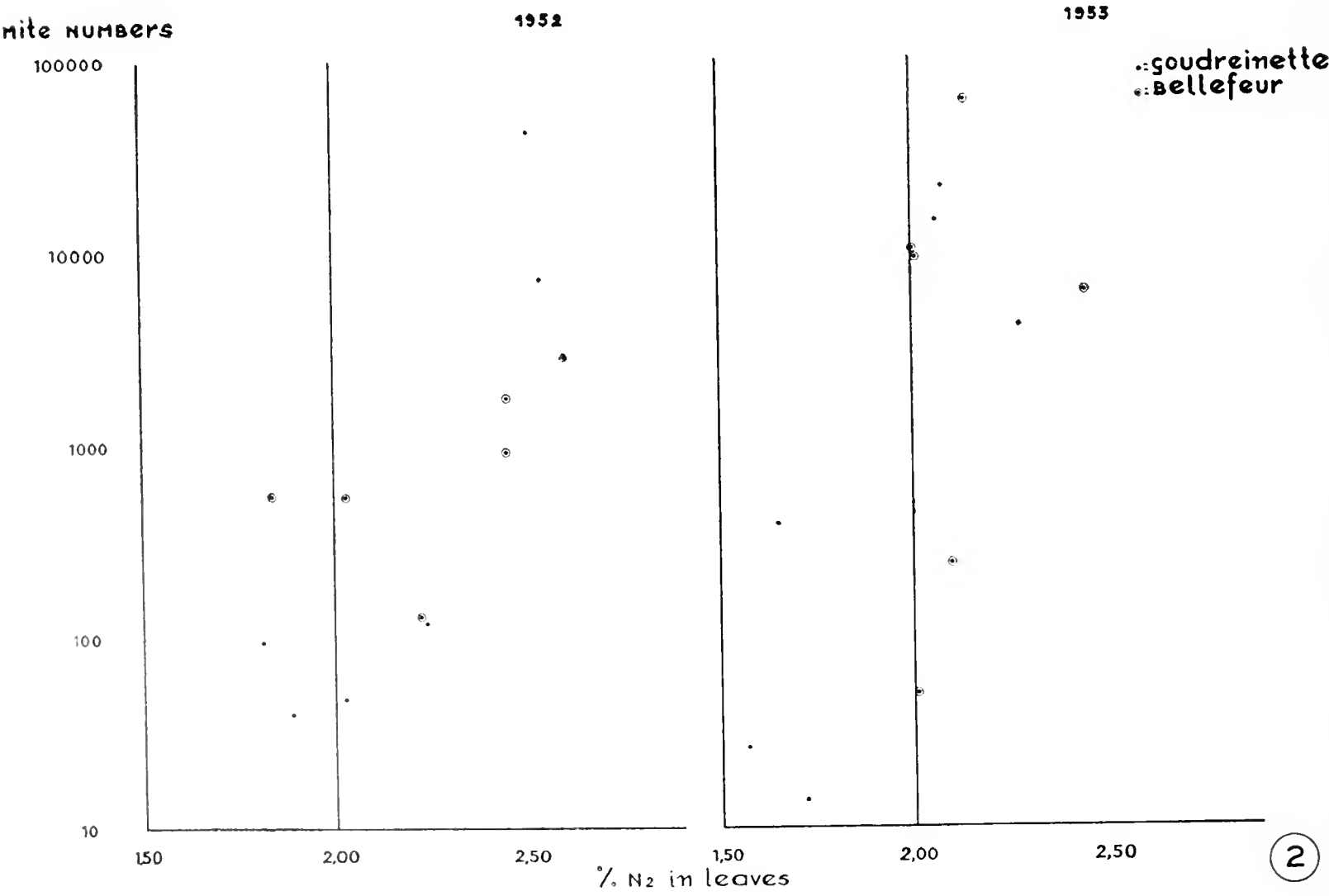
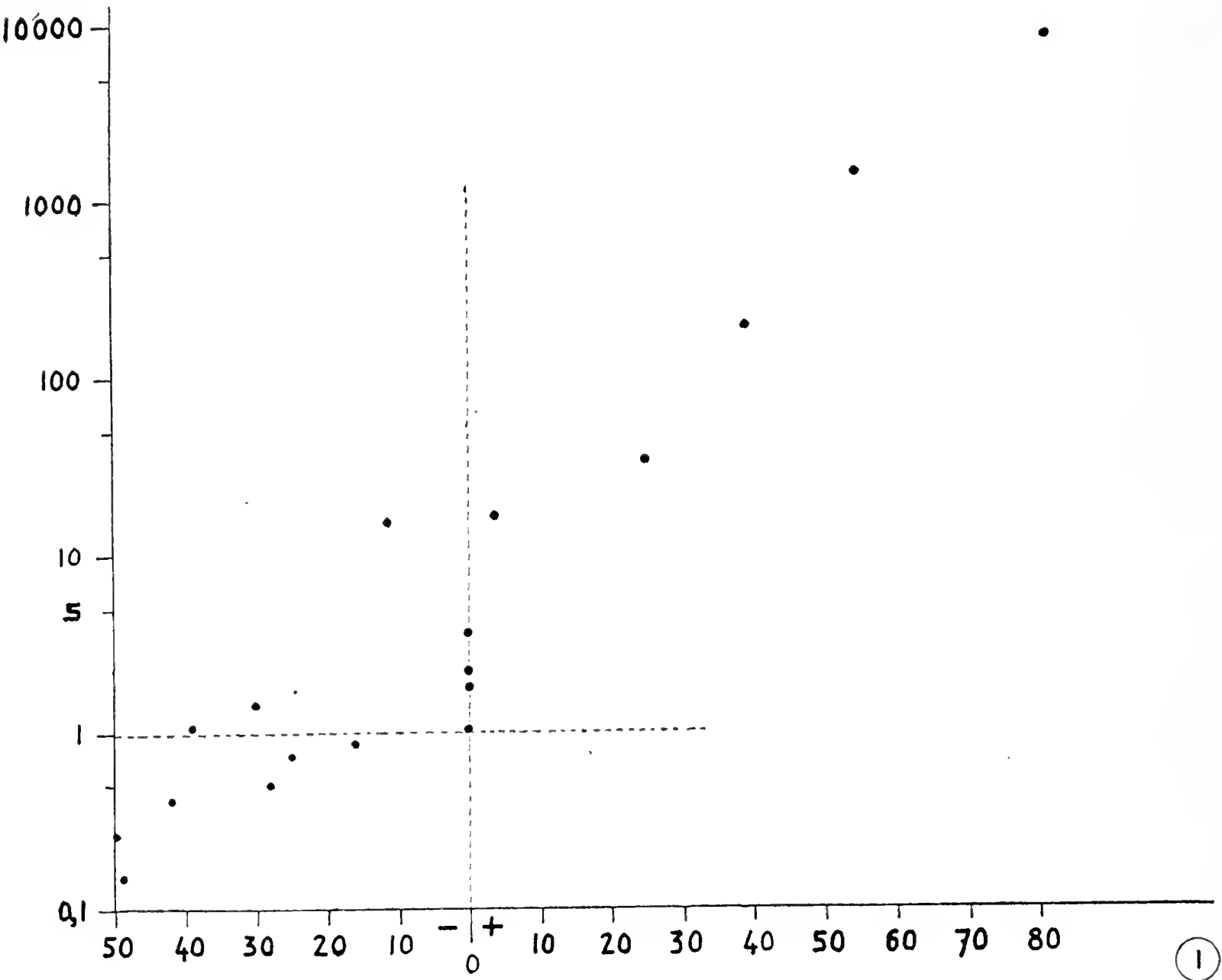
However this problem is of sufficient significance to merit further study.

STIMULATION OF EGG-PRODUCTION

Finally there is the question of DDT as a stimulant to red spider egg-production. We have already published the results of some field-observations and laboratory-



experiments on the egg-production of mites, living on leaves sprayed with DDT. This showed that the number of eggs produced per female was considerably higher when mites fed on DDT-leaves than on the control-leaves, which remained unsprayed (Hueck *et al.*, 1952).



It is perhaps of some value to mention here that the same has been shown to happen to *Calandra granaria* (= *Sitophilus granarius*). When DDT is mixed with the grain in which *Calandra* lives at very low doses this induced a higher total egg-production for groups of 30 females as compared with the controls. (Kuenen, 1958).

### CONCLUSIONS

We do not pretend that we have shown that predators are not the main factor controlling numbers of mites in orchards.

What we have tried to show is that there are a number of factors which may well have some influence, and that until the actual significance of each of these has been estimated with sufficient accuracy, it will be impossible to get a good picture of the population dynamics of *M. ulmi*. It is our aim to continue observation in a number of experimental plots, and we hope that in doing so, we will succeed in helping to unravel this very interesting and very important problem.

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### DISCUSSION

P. GARMAN. Discussion of nitrogen relation connected with mite abundance confirmed by experiments in Connecticut.

D. J. KUENEN. I was aware of the fact that DDT increased nitrogen content in certain plants. If drought increases nitrogen content of leaves, this certainly helps to bring our experience with mites in line.

- 
- ← Fig. 1. Correlation between numbers of *M. ulmi* and *Br. praetiosa* developing on small trees. Abscissa: number of days the population of *M. ulmi* appeared on the leaves ahead of *Br. praetiosa*. Negative values: *Br. praetiosa* appeared earlier than *M. ulmi*. Ordinate: ratio between numbers of each species (M/B) developing on the leaves (total population size) plotted logarithmically.
- Fig. 2. Correlation between N<sub>2</sub>-content in leaves (expressed as dry weight, and total population of *M. ulmi* in 1952 and in 1953 for two varieties of apple (Goudreinette and Bellefleur).



# The Natural Control of Phytophagous Mites on Apple Trees in Nova Scotia<sup>1</sup>

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Three species of phytophagous mites are common to apple trees in Nova Scotia. These are the European red mite, *Metatetranychus ulmi* (Koch), the clover mite, *Bryobia praetiosa* Koch, and the two-spotted mite, *Tetranychus telarius* (L.). Of the three, only the European red mite has been a serious pest. The two-spotted mite has received little attention, as it is normally found only in extremely small numbers on apple trees. The clover mite has had a varied history: for many years it was found only in abandoned orchards because the sulphur sprays that were in use in commercial orchards were destructive to it. More recently, following a change to sprays non-toxic to it, the clover mite has invaded a large number of orchards. It is, however, of minor consequence as a pest and is even presumed to be of value as a food reservoir for predators.

The climate of Nova Scotia is relatively mild and is not subject to extremes of temperature or moisture. It appears to be suitable to the mites mentioned. Although variations in weather can cause fluctuations in the numbers of mites, it is doubtful if these variations greatly influence the average population density in Nova Scotia. There is a rich growth of wild vegetation in and around the orchards which probably has an important indirect influence on the orchard fauna. The phytophagous fauna of these wild plants may act as a food reservoir for predators and all predacious species found in the orchards have been taken from the wild vegetation.

The European red mite was a constant threat in most orchards from 1929 to 1945 when sulphur was the commonly used fungicide. The change to ferbam after 1945 did not greatly alleviate trouble from this mite. The clover mite, which had previously been kept in check by the sulphur sprays began to increase in many orchards but never became a serious pest. With the introduction of DDT there followed a period in which only the use of miticides could keep the red mite in check. Glyodin which has some miticidal action and which is innocuous to predators has little beneficial influence when DDT is used with it. When glyodin was used alone a rapid reduction of the mite population took place. After 1954 most of the growers substituted ryania for DDT with the result that owing to predation, there is a very low population of the European red mite, and the clover mite is causing very little trouble. The evidence available indicates that captan is not detrimental to predators.

## THE IMPORTANCE OF PREDATION

Although many factors influence the density of phytophagous mite populations in orchards, there is now considerable evidence to show that predation is the most important factor. When predator populations are repressed by any factor that is harmless to mites an increase in the number of mites takes place. Conversely, in the presence of a high population of mites, when the repressive factor is removed the number of predators increases and the mite population declines. This concept may be illustrated by the results from an experiment in which DDT was used to destroy predators. In the experiment a number of dilutions of DDT were applied to a series of plots at several periods of the season. The applications were made in 1953 but the studies were continued in 1954 and 1955 with fungicides only being applied in the latter two years. Four dilutions of DDT were used but the data from the plots treated with one-half pound of DDT per 100 gal. will serve for purposes of illustration.

When DDT was applied in the spring (May 1, 12 and 20) of 1953 the mite population showed a marked increase but declined in the fall because of the re-establish-

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ment of predators. No further DDT was used and both mite and predator populations remained low in the succeeding two years.

Mid-summer applications of DDT (June 12, 22 and July 6, 1953) destroyed the predators at a critical period and their populations were re-established too late in 1953 to prevent heavy deposition of winter eggs of the phytophagous mites. Thus there was a high population of mites again in 1954. By late summer, however, predators were able to reduce the population. In the third year the mite and predator populations were again at a low level.

When the applications of DDT were delayed until near the latter part of the summer (July 16, 29 and August 11) the mite population was protected from predation in the fall of 1953. As a result, there was an increase in the mite population the following spring. The larger population was attractive to predators and these reduced the mite population to a low level by the fall of 1954. In 1955 the numbers of mites and predators were low.

THE PREDACIOUS FAUNA OF NOVA SCOTIA APPLE ORCHARDS

Most of the insect predators that can be rated as important in the control of mites are found in four orders. In the order Thysanoptera there are four species; in the order Hemiptera, 12 species; in the order Coleoptera, two species; and in the order Neuroptera, several species. Among the acarid predators are 14 species in the family Phytoseiidae some of which are known to prey on the pest species of mites. There are also several other Acari and numerous small spiders that have been observed to feed on phytophagous mites. There is thus a substantial number of species from which the predator fauna of an orchard may be drawn. Usually, however, a small number of species constitutes the predator population in any given orchard. The species forming the predator complex varies in composition and numbers from orchard to orchard and because of this it is impossible to list the predators in order of importance. Very broad generalizations only may be made, such as that predacious thrips will be rare on sulphur-treated trees and are apt to be common on ferbam-sprayed trees.

It is rarely possible in nature to observe the effect of a single predacious species on a mite population. The conditions conducive to an increase in the numbers of any one predator (i.e., a high mite population and the absence of harmful sprays) usually favor the increase of several. Fortunately, it was possible to observe the effectiveness of four of the natural enemies in orchards where each was the only predator present.

The results in Table I were taken from the sulphur plot of an experimental orchard in 1953. Although a single estimate of the population of *Hyaliodes harti* Knight was made on June 15, the numbers found are indicative of the population

TABLE I — Effects of *Hyaliodes harti* Knight\* on the Population of *Metatetranychus ulmi* (Koch) in the Shaw Orchard in 1953.

Date		Mites and eggs per leaf
June	1	24
	9	121
	17	213
	25	79
	30	42
July	13	72
	20	22
	27	6
Aug.	7	3

\*An average of 7 *H. harti* were observed per inside leaf cluster on June 15.

that preyed on the mites for about a month. The rapid decimation of the mite population from the attacks of this mirid is typical of orchards in which it is found in large numbers. *H. harti* is most effective at high mite densities and, since it tolerates sulphur, it was one of the most effective predators during the years when sulphur was in



common use. Because it has one generation a year and thrives best at a high density of mites, control by this mirid is highly variable.

In the Tobin orchard there was an opportunity to study the thrips, *Haplothrips faurei* Hood, where it was almost free from the competition of other predators.

TABLE II — Effects of *Haplothrips faurei* Hood on the Population of *Metatetranychus ulmi* (Koch) in the Tobin Orchard in 1947.

Date		H. faurei per tray*	M. ulmi per leaf
June	20	20	22
July	4	41	—
	17	—	98
	29	153	—
Aug.	13	111	—
Sept.	5	—	0.4
	9	65	—
	17	119	—
	29	98	—
Oct.	9	40	—

\*The predators were dislodged from the lower limbs by beating onto a cloth covered tray one square yard in area.

The European red mite was fairly abundant in this orchard early in 1947 but a large population of predacious thrips reduced it to very small numbers by fall. The thrips continued to subsist in the orchard throughout the fall and into the following year. This thrips is one of the most important insect predators found in apple orchards. Since there are several generations it may be found throughout the growing season and may appear in large numbers when mites are abundant.

In the Sawler orchard, a series of plots were sprayed nine times in 1954 and again in 1955 with weak dilutions of DDT. The results given in Table III are from

TABLE III — Effects of *Anthocoris musculus* (Say) on the Population of *Metatetranychus ulmi* (Koch) in the Sawler Orchard in 1954 and 1955.

1954			1955		
Date	A. musculus		Date	A. musculus	
	per tray	Phytophagous* mites per leaf		per tray	Phytophagous* mites per leaf
June	1	1	May	30	4
	22	2	June	20	31
July	5	3	July	7	38
	21	8		20	27
	31	24	Aug.	1	131
Aug.	16	28		18	94
	30	23	Sept.	1	29
Sept.	13	16			

\*European red mite and clover mite combined.

the plot on which one-half pound of DDT per 100 gal. was used. DDT, at this strength, eliminated all insect predators except *Anthocoris musculus* (Say), which is tolerant of low concentrations of DDT. The anthocorids prevented the rapid build-up of mites that usually follows the use of DDT but in the numbers present they were unable to prevent an increase in the mite population. It is a valuable natural enemy and like the thrips, its value is partly because it is active throughout the growing season.

Table IV illustrates an instance in Nova Scotia in which phytoseiid mites were the only important factor in the control of a phytophagous mite population. As there were very small numbers of other phytoseiids and small numbers of insect predators, predation from these was a negligible factor in the control obtained. The population of

TABLE IV — Effects of *Typhlodromus tiliae* Oudms. on the Populations of *Metatetranychus ulmi* (Koch) and *Bryobia praetiosa* Koch in the Fuller Orchard in 1955.

Date	M. ulmi	B. praetiosa	T. tiliae
July 7	3	30	13
14	18	29	14
21	30	8	20
28	10	5	17
Aug. 4	3	4	14
11	2	4	14
18	0	0.6	8
25	0.3	0.6	7

*Typhlodromus tiliae* Oudms. was unusually high and at these densities was able to reduce rapidly the phytophagous mite population. *T. tiliae* is the most prevalent phyto-seiid found in commercial apple orchards in Nova Scotia. Where spray materials that are not destructive to them are used it is usual to find this species, along with several species of insect predators, attacking the phytophagous mites.

Instances such as the above four examples where only one species of predator is responsible for the control of mites are rare. Usually several species are present but seldom more than 10 or 11. The variation in the species complex is so great that no typical example of predator-prey relationship can be given. An example of the effects of a mixed predator population on the mites in a plot treated with ferbam is given in

TABLE V — Effects of Insect Predators on a Population of *Metatetranychus ulmi* (Koch) in a Ferbam Plot in the Shaw Orchard in 1953.

Date	Total mites per leaf	Total predators per tray	No. predacious species
May 6	1	20	2
21	7	13	1
June 12	19	20	10
July 6	111	28	8
20	—	148	11
31	156	98	8
Aug. 8	48	258	9
17	5	77	8
Sept. 2	—	53	4

Table V. It also shows the numbers of insect predators per sample that may be commonly encountered, together with the numbers of species that composed the predator population.

GENERAL DISCUSSION

The rating of the importance of each of the predacious species is usually based on the economic needs for the control of phytophagous mites. Where the phytophagous mite population is threatening damage to the apple crop, usually because of the destruction of predators, those predators that are voracious feeders and that survive the sprays in use are considered to be the "important" predators. Such predators are important only because of this unnatural environment and under other spray treatments might be much less important. Where no sprays detrimental to predators have been used for several years the population of phytophagous mites is low and tends to remain so. Since this is a more desirable state the factors that maintain the mite population at a steady low density are, fundamentally, the most important. For example, the mirid, *H. harti* which is very effective against high mite populations is not likely to be an important regulating factor at low mite densities.

We are speculating as yet if we attempt to specify the factors that regulate the populations of phytophagous mites at a low level, but there is some evidence to suggest

what one of the important factors may be. Observations on the fauna of abandoned orchards are of some help in the studies. The constancy of low mite populations in abandoned orchards is a striking feature and the writers have yet to observe a single instance of a high mite population in one of them. The poor condition of the foliage of these orchards may help to inhibit the development of the phytophagous mites but is not the only factor, since the thrifty foliage of many commercial orchards using "modified" spray programs has had very light mite populations. Abandoned orchards are characterized by a great variety of predacious arthropod species, and the insect predators are usually scarce and occur quite irregularly in time and from orchard to orchard. Because of this irregularity it seems doubtful if the insect predators exert an important regulating effect on the mite infestations when the density is low. The predacious phytoseiid mites are found in abandoned orchards in fairly even densities even when the phytophagous mites are very scarce. In addition to this, they are active from early spring until late fall. If a material such as ferbam is used in an abandoned orchard, the phytoseiids are destroyed and an increase in the numbers of phytophagous mites takes place, to be followed by increased populations of insect predators. If the ferbam treatments are continued for a number of years, the fluctuations in the populations of phytophagous mites are frequently quite large. The fluctuations on trees treated with ferbam are much greater than are ever found on abandoned trees. In addition to this example, it is a fact that the spray materials that promoted large fluctuations in the mite population were destructive to the phytoseiid mites. It has not been established that the two phenomena are actually cause and effect.

The theory that sprays innocuous to predators will eliminate damage from mites has been tested on an industry basis in Nova Scotia. About 90 per cent of the growers have, for several years, used materials that are not destructive to predators. As a result, not only are mites under control but it is difficult to find orchards with significant infestations. Only in the orchards of a small number of growers who have continued to use DDT is it necessary to use control measures. Now that mites are at a very low level the numbers of insect predators are small and the numbers of phytoseiid mites are comparable to those on neglected trees.

## DISCUSSION

D. A. CHANT. Why should a predator be more effective at low prey densities than at high? Surely the same qualities are needed under either condition.

F. T. LORD. When there is a high density of phytophagous mites, typhlodromids are among the predators destroyed by the spray. In the reduction of a high population the insect predators have been the important agents, assisted by typhlodromids. At low densities of mites the insect predators almost disappear, leaving the typhlodromids. We speculate only when we assume that the continued low density is due to typhlodromids. There is little room for disagreement with your suggestions. The use of harmful sprays is what makes it impossible to answer the questions directly since the effectiveness of typhlodromids at high and low red mite density cannot be compared.

F. T. LORD. Under Nova Scotia conditions, all species of phytophagous mites are at low levels in abandoned orchards.

P. J. CHAPMAN. In New York the clover mite occurs very abundantly in some abandoned apple orchards but the two-spotted mite and the European red mite are usually present in small numbers. Clover mite rarely occurs in sprayed apple orchards but may in cherry plantings where schedule of lead arsenate and copper fungicides may be a factor.

P. GARMAN. Remarks on the effect of ground predators on the abundance of two-spotted and clover mites. Predators in the ground cover have great influence on abundance of these species.

N. H. ANDERSON. In British Columbia we have found that there is no migration of clover mite into the trees from the cover crop, hence, the predator complex on the ground is not a factor affecting the population of *Bryobia* in the tree.

E. H. SMITH. What population level of mites do you consider injurious from a commercial point of view?

F. T. LORD. We do not have a rule of thumb method. If materials destructive to predators are to be used, ten mites per leaf in the spring would be sufficient to require miticide treatment.

D. W. CLANCY. *Stethorus punctum* appears to be more resistant to DDT than five or ten years ago. We now get fairly high survival following DDT sprays, but *Stethorus* is not considered a highly effective mite predator in West Virginia.

D. A. CHANT. A combination of a predator effective at low densities (e.g. typhlodromids) and one effective at high densities (e.g. coccinellid) does not seem possible at present. In England, typhlodromids are frequently extremely abundant under derelict conditions.

C. A. FLECHNER. *Typhlodromus* mites are effective predators at low plant feeding mite populations because they can be sustained nutritionally by a very low phytophagous mite population. They cannot disperse rapidly from tree to tree to search out high mite populations.

A. M. MASSEE. DDT applied at 0.1% destroys the species of anthocorid bugs present in English orchards. None is resistant, as is the case with a Canadian species.

D. J. KUENEN. Experience in Holland supports the suggestion that typhlodromids can eliminate low populations. Coccinellid beetles can reduce high concentrations to low levels but wander off or starve at low populations.

# Some Predators of Phytophagous Mites, and Their Occurrence, in Southeastern England

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## ABSTRACT

The forty-five species of insect predators on *Metatetranychus ulmi* (Koch) and related mites in southeastern England represent a wide range of families. The species that occur either regularly or abundantly enough on fruit trees to be considered of importance number about a dozen, a high proportion of which belong to the Hemiptera-Heteroptera. The species differ in their occurrence in various types of orchard, one of the more important factors which account for the differences being the spray programme. In unsprayed orchards a large number of predators, with a varied food supply, keep phytophagous mites at a relatively low and steady level. In sprayed orchards fewer species occur, although not necessarily in lower numbers, and together with *M. ulmi* show considerable fluctuations in abundance. Most of the predators are not specific to particular food organisms or host plants, and occur naturally on a wide range of plants.

The occurrence in orchards and other habitats is described of a number of predator species, including *Blepharidopterus angulatus* (Fall.), *Campylomma verbasci* (M.D.), *Anthocoris nemorum* L., *Stethorus punctillum* Wei. and *Conwentzia pineticola* End.

In England more than forty-five insect species have been recognised feeding on the fruit tree red spider mite (European red mite), and also a large number of mites and spiders. The predacious insects belong to a wide range of families; the largest group is the Hemiptera-Heteroptera represented by the families Capsidae (Miridae), Anthocoridae and Nabidae; there are a few species of Thysanoptera; members of the Chrysopidae, Hemerobiidae and Coniopterygidae of the Neuroptera, and Coccinellidae and Staphylinidae of the Coleoptera; and also larvae of various syrphid and cecidomyid species of the Diptera.

Of this large number of species which have been observed feeding on mites, many are of relatively little importance; they may be present only occasionally, or in small numbers, or, while favouring some other form of food, they may only feed incidentally on mites e.g. the large coccinellids. Of those that have been found abundantly, some are to be found only in neglected and unsprayed conditions, a few are found only in sprayed orchards where mites are abundant; other species vary from year to year with natural fluctuation, while some occur only in hot seasons. In studying the occurrence of these predators the main comparison has been between commercially-sprayed orchards and completely untended, neglected orchards. The number of species present there, and their relative importance are very different in these two types of habitat, and among the reasons for these differences the following factors, operating usually in commercial plantations, must be considered: (1) the spraying programme (2) pruning operations, thinning and spacing of trees (3) application of organic and inorganic fertilizers (4) the removal of undergrowth leaving in some cases a grass cover, and in others bare soil (5) alternative sources of food supply are lost owing to spraying and cultivation, and on the trees themselves lichens, *Pleurococcus* etc. are removed (6) competition between species is changed. Of these factors most work has been done on spraying materials and their direct effects, and much less on such subjects as cultural practices and the influence of hedgerows. Knowledge of the host-plant range, and food preferences is necessary if an explanation is to be found of the differences in fauna of the two types of orchard.

As a result of all these factors the main differences between sprayed and neglected orchards as far as the fruit tree red spider mite and its predators are concerned are, firstly, that the red spider is at a steady, and low, density in neglected orchards and does not vary from year to year, whereas in commercial orchards it fluctuates wildly sometimes reaching high levels, and is very variable from year to year; Secondly, predators are many in species, but individual species are not great in numbers



in neglected conditions, whereas in commercial orchards predators are few in species, but may sometimes be very abundant, and vary greatly from year to year.

Half a dozen predacious insect species are at times abundant in commercial orchards and for this reason are considered important at the moment.

*Blepharidopterus angulatus* (Fall.), the black-kneed capsid, is common throughout Europe, and although often found on fruit trees has not elsewhere been noted as predacious. It has been recorded in North America once, but apparently has not become established there. In England it is a common insect, by no means specific to fruit trees; it is found on a wide range of plants over most of the country, mainly on trees such as alder, willow, oak, elm, hornbeam, maple and hazel, and also on rosaceous plants sloe, hawthorn and all varieties of *Pyrus* and *Prunus*. It is common in orchards, and occurs on neglected apple and plum trees as one capsid species among several. Although many mirids originally occurred in orchards, by 1945 this species was the only remaining species in most commercial plantations and in many was very abundant. The reason for this may be that the eggs are more resistant to sprays than some others, it is a relatively late hatching species, or that it is better able to survive orchard conditions such as open trees and no undergrowth, features which doubtless discourage some species. An interesting point is the hatching in the two types of orchard: in commercial orchards the black-kneed capsid starts hatching in late May and early June whereas in unsprayed it does not hatch until late June or July; the reverse is true of the fruit tree red spider mite, which hatches earlier on unsprayed trees.

Like most of the predacious mirids it is also partially phytophagous, but is mainly animal feeding. It is able to feed on a variety of food, for example aphids, caterpillars, various mites. It is exceedingly active and will attack other predatory species and even members of its own species. In many commercial orchards where mites may be the only available food in the summer months, the black-kneed capsid becomes closely related to red spider density within a limited area. Large fluctuations occur from year to year, giving mite control for up to three summers, followed by two or three years with no control. It is unfortunate that the mirid has only one generation a year, and therefore cannot increase rapidly in response to increased food supply, and that its relatively late appearance in the summer allows two generations of red spider before it hatches.

The black-kneed capsid became established in English orchards under the old routine spray programme of winter-wash, either tar oil or a dormant DNC-petroleum, and summer applications of lime-sulphur, nicotine, lead arsenate and derris, and later, spring applications of DDT. With the introduction of parathion and TEPP for red spider control, it was exterminated in many orchards, but since the change from these highly toxic materials to sprays such as chlorbenside and chlorfensone it is encouraging to find the insect moving back into orchards, increasing and becoming established again. It is only in the few orchards where DDT is applied in midsummer for codling moth control that it is now necessarily absent.

A subject not studied yet in detail is the question of enemies and regulation of beneficial insect populations, although it is known that they feed on each other to a certain extent both within and between the species. One parasite of mirids has been found to occur quite commonly, a braconid, *Euphorus apicalis* Curtis. The larva feeds in the abdomen of mirid nymphs and emerges, usually from the fifth instar nymph but occasionally from the adult, drops to the ground and pupates within a white cocoon. It is found in the late maturing nymphs, it probably causes a slowing of their development. It has been found in the black-kneed capsid, also *Psallus ambiguus* (Fall.), *Malacocoris chlorizans* Pz., *Plagiognathus arbustorum* F., and found emerging from mid-June until mid-August. Adults emerge from the cocoons in the following May or June. Parasitized black-kneed capsid nymphs have been found commonly in unsprayed orchards, and in hedgerow trees and bushes, and less commonly in commercial orchards.

*Campylomma verbasci* (M.-D.) is another mirid species which is often abundant; in North America it is known as the mullein leaf bug and has been found there to cause considerable damage, although at the same time was found to be predacious. It has not been recorded previously in England or on the Continent on fruit trees, and it seems

that in England it may only recently have appeared on fruit trees. It has not been found to cause any damage, and is a useful predator. It was widespread and abundant in commercial plantations of south-east England until the introduction of the phosphorus insecticides, although somewhat seasonal in occurrence. Although abundant in commercial plantations, it occurs only occasionally in small numbers on unsprayed trees; possible reasons for this are that it needs a higher density of food than is normally found on unsprayed trees, or that the rather small nymphs are unsuccessful in competition with the larger mirids and voracious anthocorids and nabids abundant under these conditions. It is unique among the predacious mirids found on fruit in that it has two generations a year. It hatches relatively early, starting in May, and with the development of the second generation in July may become very abundant then. Apart from fruit trees it is found on oak (*Quercus*), as well as on such plants as *Verbascum*, but is certainly rather restricted in host plant range, as well as being spasmodic in occurrence from year to year.

*Anthocoris nemorum* L. is an insect of widespread occurrence in Great Britain and throughout Europe in orchards and on many other host plants. It overwinters as an adult, is active from March or April until October, passing through two generations. In spring it is an important predator feeding on aphids, apple sucker, caterpillars and mites as they are emerging. It is largely predacious in habit, extremely voracious and hunts actively for its prey. It occurs on many trees and plants, moves readily, is tolerant to weather conditions, and therefore rapidly reinfests orchards after it has been eliminated by harmful sprays. Another species of the family Anthocoridae, *Orius majusculus* Reut., of very similar habits, is also often abundant in English orchards, but is somewhat less regular in occurrence.

*Stethorus punctillum* Wei. is a small coccinellid which occurs throughout Europe associated with red spider mite populations. In England it is spasmodic in occurrence; it occurs in large numbers in orchards where red spider mites are abundant and in relatively hot summers, but in cool summers or where mites are not plentiful, it is scarce. It overwinters as an adult, and although these may become active as early as April, they are rarely found in any numbers laying eggs until late May and June. When conditions are favourable it increases very rapidly and may become very abundant by August. It is not found on many other host plants, in small numbers on sloe and hawthorn. Thus this species, under conditions in south-eastern England, is very restricted, and as it depends on high mite density and high summer temperatures it is of limited value. It is rarely found on unsprayed trees.

*Conwentzia pineticola* End. (Neuroptera, Coniopterygidae) is also restricted in occurrence, depending on high summer temperatures and a fairly high density of mites. However, when conditions are favourable it increases very rapidly and becomes very abundant in late summer. It can pass through three generations in a season, the final larvae feed late in the autumn, sometimes into December, on the winter eggs of the fruit tree red spider mite. Winter is spent in the prepupal stage in a white cocoon. They feed only on mites, and have not been found on other host plants. Further study is needed of this species, and of *S. punctillum*, both of which are occasionally of great importance. Study of their food requirements and preferences, host plant range, optimum climatic conditions, and natural enemies would indicate the limiting factors of these spasmodically occurring species.

In our present state of knowledge of the fluctuations of phytophagous mites on fruit trees in England, it appears that the problem is the preservation of the predacious insects and mites that normally occur in orchards. Importation of new species is not necessary where the natural fauna is so rich, and the indoor breeding and subsequent release of beneficial species would be valueless while the present orchard spraying programmes continue, as it is these which result in the inadequate predacious fauna. Reservoirs of most beneficial species occur on alternative host plants in hedgerows, ditches and woodlands and soon invade orchards after spray applications have eliminated them. The problem then is not to find enough predators to control phytophagous mites, but to preserve them while at the same time controlling the fungal diseases and insect pests as well. Study of the natural enemies of some insect pests, for example aphids, caterpillars, and apple sucker might show that these pests also are

at least partially amenable to natural control measures, and hence lead to reduction in the number of insecticide applications needed. However, when advantage is taken of all the beneficial insects, it is obvious that for the production of high quality fruit spraying applications will always be needed for control of fungal diseases and some insect pests. In sprayed orchards it is the early season predators that are lacking as these are killed off each year by winter or spring spray treatments. The species which could operate in the spring if not killed by sprays belong to three groups: the Anthocorid bugs which come out of hibernation in March and April; the mirid species *Psallus ambiguus* (Fall.) which hatches in April, and the predacious Typhlodromid mites which become active in March and April, and appear to be most valuable in spring. At the moment there are fungicides on the market which are relatively non-toxic to beneficial species compared with the traditional lime-sulphur, and when these are used in conjunction with a reduced insecticide programme they result in lower phytophagous mite densities and higher predator populations. Further study of the long-term effects of recognised spray chemicals may show that it is possible to preserve more beneficial insects, now that their value and habits are more fully understood.

# Natural Enemies of Tetranychid Mites on Citrus and Avocado in Southern California<sup>1</sup>

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## ABSTRACT

Mite pests of avocado (six-spotted mite *Eotetranychus sexmaculatus* (Riley) and avocado brown mite *Oligonychus punicae* (Hirst)) are under satisfactory natural balance in most avocado-growing areas of California. This balance is maintained largely by several species of predators. The balance is readily upset by the removal of these predators by hand picking or by the use of insecticides which act more severely against the natural enemies than against the mites. The most effective predators of avocado mites are *Typhlodromus* mites (several species), *Stethorus picipes* Casey, *Oligota oviformis* (Casey), and the itonid *Arthrocnodax occidentalis* Felt. Of these predators, the *Typhlodromus* are the most effective at low host-mite populations and *S. picipes* is the most effective at high mite populations.

The citrus red mite *Metatetranychus citri* (McG.) is in satisfactory natural balance in some citrus growing areas of California. More generally, however, the necessity of insecticidal treatment for other pests frequently disrupts this balance. The most effective predators of the citrus red mite are *Typhlodromus* mites (several species) and *Stethorus picipes*. *Oligota oviformis* is sporadically effective in reducing citrus red mite populations. On occasion, when there are sufficient populations of honeydew-secreting insects in the groves, dustywings, green lacewings, and various coccinellids may be of importance in maintaining plant-feeding mites at low populations.

## THE CITRUS RED MITE

The citrus red mite, *Metatetranychus citri* (McG.), is one of the major pests of citrus in southern California. However, in certain restricted areas this mite is generally kept under satisfactory natural balance by a complex of predators. This is especially true in the interior of San Diego, Ventura, and Tulare counties. In most other areas, from one to three acaricidal treatments are applied yearly for the control of this mite. The widespread need for chemical control of the citrus red mite is no doubt due to periodic insecticidal treatments required to control other citrus pests. Such treatments reduce the numbers of mite predators and thus prevent satisfactory natural control of the mites.

Repeated field experiments have shown that in groves where all insecticidal treatments were withheld for a year or more the ratio of predators to mites was increased and mites were frequently brought under satisfactory natural balance. If it were not for the use of insecticides to control other citrus insects, increased predator efficiency would greatly reduce the status of the citrus red mite as a pest of citrus in southern California.

Despite the adverse effect of insecticidal treatments, various species or complexes of predators frequently control mite populations or check their increase sufficiently to permit extension of the time interval between treatments. The benefit derived from predators in this respect is of great economic importance to citrus growers.

## THE SIX-SPOTTED MITE AND THE AVOCADO BROWN MITE ON AVOCADO

A complex of predators generally keeps the mite pests of avocado, namely, the six-spotted mite, *Eotetranychus sexmaculatus* (Riley), and the avocado brown mite, *Oligonychus punicae* (Hirst), in satisfactory natural balance in most avocado-growing areas of southern California. This crop wise control of mites by predators occurs because, in general, all other avocado pests are also under satisfactory natural balance. Thus balance-upsetting insecticidal treatments are rarely necessary.

<sup>1</sup>Paper No. 1006, University of California Citrus Experiment Station, Riverside, California.

It has been demonstrated repeatedly, however, that various factors which inhibit predator activity may cause a rapid development of high mite populations. Applications of long-residual insecticides have been especially serious in this respect.

### PREDATORS OF MITES

The same complex of predator species is found in both citrus and avocado groves. The most effective predators, listed in their approximate order of importance, are the following:

Predator	Tetranychid Mites as Food Source
1. Laelaptidae	
<i>Typhlodromus finlandicus</i> (Oudemans)	Primary
<i>T. conspicuus</i> (Garman)	Primary
<i>T. longipilus</i> Nesbitt	Primary
<i>T. sp.</i> , near <i>finlandicus</i>	Primary
<i>T. similis</i> (Koch)	Primary
<i>T. masseei</i> Nesbitt	Primary
<i>T. pomi</i> (Parrott) <sup>2</sup>	Primary
<i>T. pini</i> Chant <sup>2</sup>	Primary
2. <i>Stethorus picipes</i> Casey	Primary
3. <i>Oligota oviformis</i> (Casey)	Primary
4. Coniopterygidae	
<i>Conwentzia nigrans</i> Carpenter	Secondary
<i>Parasemidalis flaviceps</i> Banks	Secondary
<i>Coniopteryx angustus</i> Banks	Secondary
5. <i>Chrysopa californica</i> Coq.	Secondary
6. Coccinellidae	
<i>Hippodamia</i> spp.	Secondary
<i>Adalia bipunctata</i> (L.)	Secondary
<i>Coccinella californica</i> Mann.	Secondary
<i>Cycloneda sanguinea</i> (L.)	Secondary
<i>Olla abdominalis</i> (Say)	Secondary
7. <i>Arthrocnodax occidentalis</i> Felt	Primary
8. <i>Scolothrips sexmaculatus</i> (Perg.)	Primary

This rating of importance, which is to be taken only in a broad sense, may vary considerably in different localities or under changing environmental conditions within a given locality.

The order of importance of predator species given here differs somewhat from that given in an earlier paper (DeBach, Fleschner & Dietrick, 1950), largely due to the fact that the earlier field studies were made in a restricted area and at a time when there was insufficient biological data on some of the species.

(1) *Typhlodromus* mites: Although different species of *Typhlodromus* mites may vary strikingly in habitat and food preferences, all of those mentioned above prey on all three species of tetranychid mites discussed in this paper. They also feed on a wide variety of species of other mite families and on immature stages of various insects.

Under favorable environmental conditions *Typhlodromus* mites are the most efficient predators for maintaining the plant-feeding mites at very low populations. Under such conditions the actual number of *Typhlodromus* mites per unit area may exceed the number of host mites. *Typhlodromus* mites are quite susceptible to various insecticides and acaricides and because of their relatively poor powers of dispersal they are slow to become re-established in groves where they have been eliminated by such treatments.

<sup>2</sup>The identity of these species is questionable. Further study may show that other species are involved.



*Typhlodromus* mites tend to avoid exposure to sunlight and consequently remain on the undersides of leaves or in other secluded areas during the daylight hours. After sunset, however, they become more active and enlarge their area of search to include upper leaf surfaces and exposed young twig terminals. This habit of *Typhlodromus* mites should be kept in mind when field-sampling techniques are being developed.

(2) *Stethorus picipes* Casey: In feeding habits *Stethorus* is practically restricted to tetranychid mites. It is equally effective in all areas of southern California where citrus and avocados are grown. *Stethorus* is by far the most effective predator in bringing high mite populations under control. Adults of *Stethorus* have excellent powers of dispersal. When mites are scarce *Stethorus* actively flies from tree to tree or from grove to grove in search of food. When relatively high populations of mites are found, *Stethorus* remains in the area to feed and reproduce. Laboratory studies have shown that *Stethorus* attains maximum ovipositional rates only when mite eggs are abundant; when adult mites are abundant but mite eggs are scarce, few eggs are laid by *Stethorus*. Laboratory studies have also shown that the rate of development of *Stethorus* larvae is more or less directly proportional to the number of mites or mite eggs consumed.

In brief, *Stethorus* adults actively search for high mite populations. The greater the abundance of mite eggs (to a given point), the more rapid the rate of reproduction of *Stethorus*. The more dense the mite population, the quicker the development of *Stethorus* larvae and thus the more generations produced in a given period of time. In addition, in comparison with other mite predators both adults and larvae of *Stethorus* are relatively resistant to most insecticides now in general use. This combination of factors makes *Stethorus picipes* consistently the most effective predator for seeking out and controlling rapidly developing or high tetranychid mite populations.

(3) *Oligota oviformis* (Casey): As a mite predator, *Oligota oviformis* is somewhat erratic. It may be fairly effective in a given grove at one time and of no consequence at another. In general it is more effective in coastal areas than in interior areas. Recent life history studies have shown that pupation takes place in the soil. This may be a partial explanation of its spotty distribution, as the condition of the soil in the groves largely determines the proportion of larvae that can find suitable pupation sites. Groves with an abundance of undisturbed leaf mulch offer better pupation sites than groves with bare ground or than groves which are cultivated frequently.

(4) *Coniopterygidae*: Earlier workers on mite predators in California recognized only one species of the *Coniopterygidae*, or dusty wings, which was referred to as *Conwentzia hageni*. Recent studies, however, have shown that three species of dusty wings are commonly found in citrus and avocado groves and that *C. hageni* is not one of them. The dusty wing previously referred to as *C. hageni* has been determined as *C. nigrans* Carpenter. The other two species are *Parasemidalis flaviceps* Banks and *Coniopteryx angustus* Banks.

It was thought until recently that tetranychid mites were the primary food of these dusty wings. Laboratory studies have shown that although both adults and larvae readily prey on mites, neither can survive on mites alone. The larvae readily develop to adult stage, however, when restricted to a diet of any one of a number of species of armored or unarmored scale insects. Adult dusty wings die within a few days when restricted to a diet of mites. If sugar is added to this diet, however, they will live and reproduce well.

With sugar from honeydew-secreting insects available, the adults will live and reproduce well on a diet of any one of a number of species of scale insects. Since neither dusty wing larvae nor adults can survive on mites alone, but since both do well on honeydew-secreting scale insects alone, it seems that such scale insects should be considered their primary food.

Results of numerous field experiments bear out this contention, as there is generally close correlation between population changes in honeydew-secreting scale insects and dusty wings. On the other hand, there is poor correlation between changes in mite and dusty wing populations.

At times, however, where there is a low but widespread population of honeydew-secreting insects to supply necessary supplementary food, dusty wings may be an important factor in the biological control of citrus and avocado mites.

(5) *Chrysopa californica* Coq.: Of the several species of green lacewings found in citrus and avocado groves, only one, *Chrysopa californica*, is of significance as a mite predator. The larvae of *C. californica* have a very wide host range including various stages of development of many species of mites and insects. The adults, however, feed only on various sugars, especially honeydews and nectars. Therefore, as in the case of dusty wings, if there is no source of sugar available in the groves there can be no sustained green lacewing population.

Laboratory studies by Hagen (1950) showed the ovipositional rate of *C. californica* to be determined primarily by the protein content of synthetic fluid foods. Ovisorption in adults fed only on honey indicated a protein need. The addition of various proteins to honey markedly increased fecundity and longevity. Thus it would be expected that protein content of the various natural sugars found in the field would similarly influence the fecundity and longevity of *C. californica* adults.

In the laboratory, green lacewings have, with some difficulty, been reared from egg to adult on a diet of mites alone. The larvae are excellent searchers and may consume large numbers of mites daily. At room temperature, with a surplus of mites, last-instar larvae consume between 1,000 and 1,500 female citrus red mites daily. In preference to mites, however, green lacewing larvae prey on many soft-bodied insects such as aphids and mealybugs. For this reason they may be of little importance as mite predators when there is an abundance of other host species. If, however, a fair population of green lacewings has developed on other hosts which are brought under control, the remaining green lacewings may then work effectively on mite populations. Also, if there is a low but widespread distribution of honeydew-secreting insects as supplemental food for green lacewings, they may be an important factor in maintaining mites at a low population.

(6) *Coccinellidae*: Several species of coccinellids, other than *Stethorus picipes*, previously discussed, prey on mites in citrus and avocado groves. Those most commonly observed are *Hippodamia* spp., *Adalia bipunctata*, *Coccinella californica*, *Cycloneda sanguinea*, and *Olla abdominalis*. As these coccinellids are primarily seeking foods other than mites, such as aphids, nectar, or pollen, it is indeed difficult to evaluate their effectiveness accurately as mite predators. Several examples will illustrate this point.

In one instance adults of *Hippodamia convergens* Guer. and *C. californica* were very numerous in a citrus grove in Orange County. The trees were in full bloom, and the coccinellids were actively moving from blossom to blossom in search of nectar. No eggs were being laid. There was a relatively low population of citrus red mites in the grove, but the coccinellids showed no interest in them. Even when some of these beetles were confined in a test tube with leaves bearing mites, they paid no attention to the mites. At this time they were apparently primarily seeking nectar. Yet it is known from other studies that at times both of these species of coccinellids prey readily on mites. As the blossom period began to wane, the coccinellids daily swarmed out of this grove in great numbers. At no time were they effective in reducing the citrus red mite population in the grove.

In another instance, however, in a citrus grove in Puente, ashy-gray lady beetles, *O. abdominalis*, were primarily responsible for controlling a developing population of citrus red mites. In this case the coccinellids came to the citrus groves in large numbers from a neighboring walnut grove infested with aphids. The females were heavy with eggs and oviposited readily on the citrus trees. A high larval population soon developed. Both adults and larvae fed primarily on citrus red mites, and the mites were soon brought under control.

This high degree of mite control by coccinellids, other than *S. picipes*, is very unusual, for they are commonly of moderate or little consequence as mite predators in citrus and avocado groves.

(7) *Arthrocnodax occidentalis* Felt: The larvae of this itonid fly are fairly effective mite predators in coastal areas where six-spotted mites occur. The colonies formed by six-spotted mites on the lower leaf surfaces seem to offer the best feeding conditions for these larvae, which are, for this reason frequently effective in controlling the six-spotted mite. They are less effective, however, as a predator of the citrus red mite or avocado brown mite, which are usually found in greater numbers on the upper leaf surfaces.

(8) *Scolothrips sexmaculatus* (Perg.): This predaceous thrip is generally of little or no consequence as a predator of tetranychid mites on citrus and avocado trees. On rare occasions, however, it may develop in large numbers and be primarily responsible for controlling mite populations. It has been observed on several occasions to be exceptionally effective in the Corona and Upland citrus areas. The reasons for this infrequent appearance of large numbers of *S. sexmaculatus* are not fully understood.

Many other species of predators, such as *Orius tristicolor* (White) and *Leptothrips mali* (Fitch), are occasionally encountered in citrus and avocado groves, but they add little to the efficacy of the predator complex herein discussed.

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- Hagen, Kenneth S. 1950. Fecundity of *Chrysopa californica* as affected by synthetic foods. *Jour. Econ. Ent.* 43(1): 101-4.

### DISCUSSION

F. G. HOLDAWAY. Comment on remark by C. A. Fleschner to the effect that citrus trees grown in one soil were more attractive to chrysopid egg deposition than were trees grown in the other soil. In 1947, when collecting ladybird beetles (*Orcus chalybeus*) in California for shipment to Bermuda, large numbers of ladybird beetle were found on a peach tree on which there were no prey. In 1955, Rudolph T. Franklin, a graduate student working with me at the University of Minnesota has observed high per cent parasitism of European corn borer by the tachinid *Lydella stabulans*, average 40 per cent, of borers in one single cross of corn, and low per cent parasitism, averaging about 20 per cent parasitism of borers in another single cross of corn. These two observations suggest that in the first case the predator was attracted to the plant, not prey; in the second case, the parasite was apparently attracted to one single cross more than to the other since the number of host larvae in the two single crosses of corn plant was the same.



# Predators and Parasites of Citrus Mites in Florida<sup>1</sup>

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## ABSTRACT

Natural control of phytophagous mites injurious to citrus in Florida appears to be dependent on the density of predatory arthropods and parasitic fungi. Weather conditions exert a strong influence on the degree of such control. No attempt is made, at present, to manipulate these natural control factors, although certain acaricides and insecticides are known to be deleterious.

*Phyllocoptruta oleivora* (Ashm.) is decimated during late summer and early fall by *Hirsutella thompsonii* Fisher, but control is not sustained. No consistent relationship between this mite and its known predators has been demonstrated.

*Metatetranychus citri* (McG.) is rapidly reduced by an *Entomophthora* following repeated rains or heavy dews. Such population reductions are prolonged except where complicated by acaricidal applications of sulfur. Statistically significant relationships between certain predatory acarina and this mite are indicated in recent data. Another fungus, *Hirsutella* sp., has also recently been found.

Spring infestations of *Eotetranychus sexmaculatus* (Riley) are heavy, following low December temperatures and light, following high December temperatures. Populations of predatory phytoseiids appear earlier in light years indicating an adverse effect of cold weather on natural control of this mite. Populations of other predators have also been correlated with those of this mite. A parasitic fungus, *Hirsutella* sp. is also known.

*Eutetranychus banksi* (McG.) is known to be attacked by *Entomophthora*. Circumstantial evidence that this mite is naturally controlled by a fungus, has recently been obtained.

*Brevipalpus phoenecis* (Geijskes) infestations have been negatively correlated with predatory phytoseiid populations, but this mite is usually a minor problem owing to the widespread use of sulfur as an acaricide.

Six species of phytophagous mites are known to attack citrus in Florida. Five of these: the citrus rust mite, *Phyllocoptruta oleivora* (Ashm.); the citrus red mite, *Metatetranychus citri* (McG.); the six-spotted mite, *Eotetranychus sexmaculatus* (Riley); the Texas citrus mite, *Eutetranychus banksi* (McG.); and the false spider mite, *Brevipalpus phoenecis* (Geijskes), are sufficiently common and widespread to demand attention. The first three species have been the subject of several natural and biological control investigations and some information on factors influencing their natural control is available. The latter two have not been studied intensively, but some natural control data have been accumulated in recent years.

The present paper represents an attempt to compare, integrate and evaluate published and unpublished data on the natural control of these five mites. Studies conducted by the author have been mainly ecologic and conducted under field conditions in widely scattered citrus groves. Much of the resultant data have been circumstantial, but in several instances direct evidence has been obtained. When and wherever possible such data have been subjected to statistical analyses, but in many cases direct comparison of population trend lines has been the only possible method of analysis.

## METHODS OF COMPARISON AND EVALUATION

Comparative data on the influence of natural control factors on mite populations and the effects of chemical treatments on such factors were obtained by using split plot techniques. Nine groves, one in the east coast citrus area, two in the north central, five in the south central and one on the west coast, were utilized. Each grove was split into two to four plots and placed under different cultural or insect and mite control programs. In all but two groves the several cultural or control programs were conducted by the grove owners under conditions of commercial production. The two exceptions

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were state owned groves wherein the control programs were conducted under experimental conditions.

Four randomly selected sample trees were located in each plot. Samples consisted of 40 randomly picked leaves, 10 from each sample tree. Plots were sampled once a month and the samples were examined in the laboratory under a dissecting microscope. Counts were made as will be indicated under the sections dealing with the several species of mites.

Because of the colonial habit of the six-spotted mite, a special sampling and counting technique was used for that species (Muma 1955a). Five to eight groves were utilized to obtain each season's data on six-spotted mites.

**CITRUS RUST MITE:** The citrus rust mite is the only eriophyd known to attack citrus in the state. It is also the most common and injurious mite found in the groves and as a result has been the subject of much research.

Populations of rust mites have been reported to increase following the application of fungicidal sprays containing copper (Winston *et al.* 1923, Thompson 1940, and Griffiths and Fisher 1950) and nutritional sprays containing zinc (Griffiths and Fisher 1950). The existence of a natural control factor, probably a fungus, has been inferred in such reports. Almost coincidental with these early residue studies, dead rust mites containing "fungous bodies" and "filaments" were described and discussed (Speare and Yothers 1924, and Yothers and Mason 1930). A more recent epizootic of rust mites associated with fungus hyphal bodies and mycelia has also been reported and discussed (Fisher *et al.* 1949). The mycelial structures and spores noted in the latter case were described as *Hirsutella thompsonii* Fisher (Fisher 1950). Although this fungus has never been proved to be the same as that represented by the internal hyphal bodies, dead mites containing hyphal bodies consistently develop mycelia of *H. thompsonii*. As a result much discussion has developed around this relationship and the possible effects of fungicides on disease incidence and mite populations (Fisher 1950a, Griffiths and Fisher 1949 and 1950, and Muma 1955a).

Although most of the literature dealing with the natural control of the rust mite has stressed the role of fungi, a few papers have mentioned predators and the effects of insecticides. The first predators observed feeding on rust mites were itonidid larvae (Hubbard 1883). In addition to these midge maggots, *Stethorus nanus* Lec. and *Chrysopa* sp. have been reported to feed on, but not reduce the numbers of, rust mites (Yothers and Mason 1930). Recently a mealywing, *Coniopteryx vicina* Hagen has also been found to feed on rust mites with no observed effect on mite density (Muma 1955a). Although populations of known predators are usually low and apparently ineffective, it has been found that trees sprayed with DDT produced significantly higher numbers of mites than unsprayed trees (Griffiths and Thompson 1947). This would indicate that some effective, possibly unknown, predator does exist.

During the present study, the numbers of healthy and diseased rust mites were counted on a microscope field basis. All healthy and diseased mites in four, wide, 13X fields, two on the upper and two on the lower surface of each sample leaf, were counted with the total computed and utilized as a population figure per leaf. The total number of known or suspected predators on each sample leaf was counted.

Data collected over the past four years demonstrate that rust mite infestations in unsprayed groves attain one or two peaks of population during a year. The highest, most sustained and most consistent occurs during the wet summer months of July, August and September, with, in many years, a secondary peak in December, January and February. Rust mite infestations in a citrus grove at Fort Pierce, Florida have exemplified this periodicity (Fig. 1). During 1954-55 only one peak of population occurred whereas in 1955-56 two peaks were attained.

There is direct evidence that a fungus disease is a major factor in the control of rust mite populations. Increases in numbers of rust mite are invariably followed with increases in the incidence of *H. thompsonii*. This phenomenon occurs regardless of citrus variety or grove location and has been consistent in all experimental groves over the past several years (Figs. 1-3). It is of significance that although chemical treatments may or may not be effective in controlling rust mite, they do not prevent

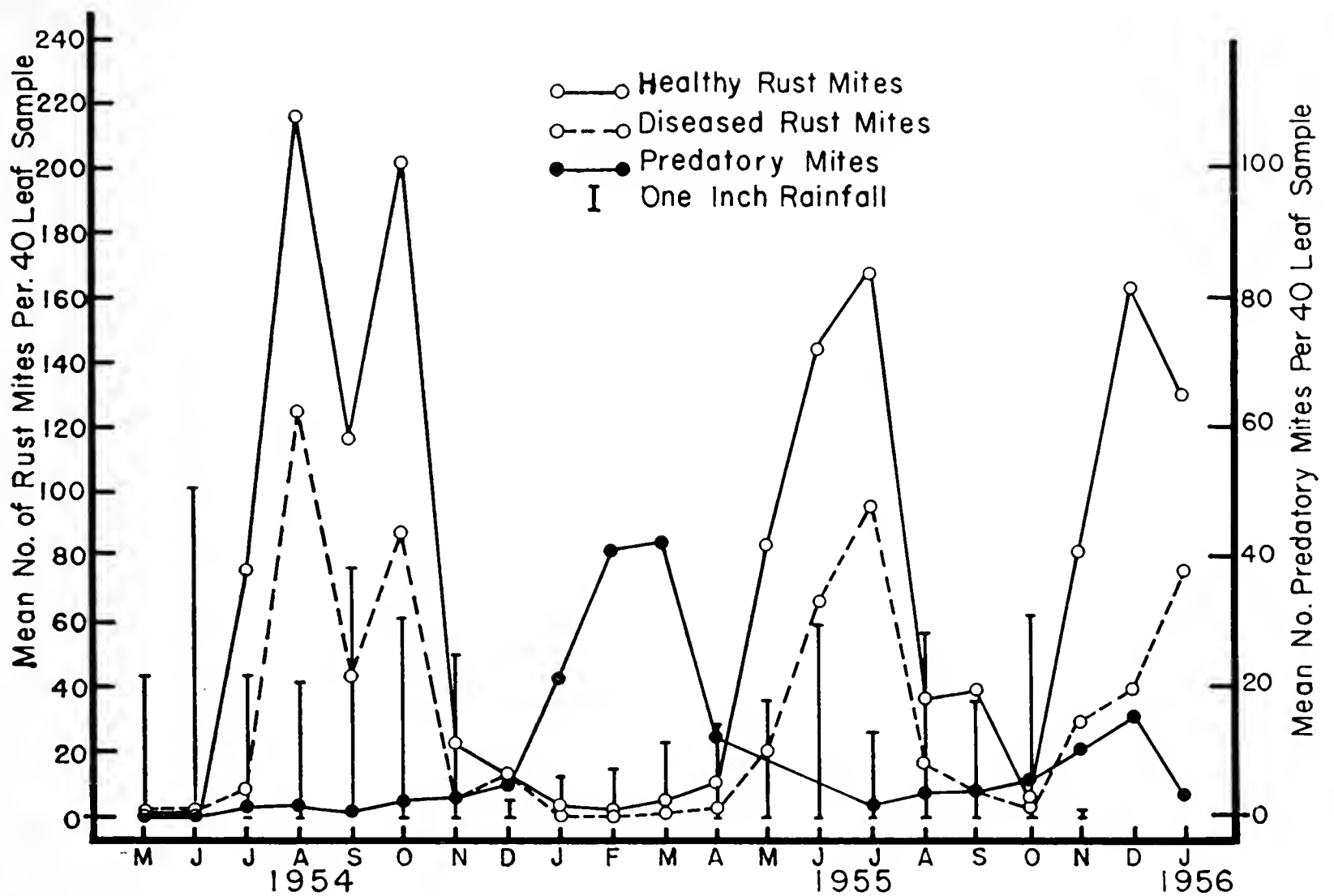


Fig. 1. Comparative populations of healthy and diseased rust mites and predatory phytoseiid mites of the genus *Typhlodromus* from May 1954 to January 1956 under varying amounts of rainfall in an unsprayed grove of Valencia oranges at Fort Pierce, Florida.

an increase in incidence of disease when mite populations increase (Figs. 2-4). From this it may be deduced that the acaricide, sulfur in this instance, has little or no fungicidal effect or that mite density has the strongest influence on disease incidence. As it has been shown that sulfur has a fungicidal effect on entomogenous fungi (Fisher and Griffiths 1951), it is probable that the latter deduction is more accurate.

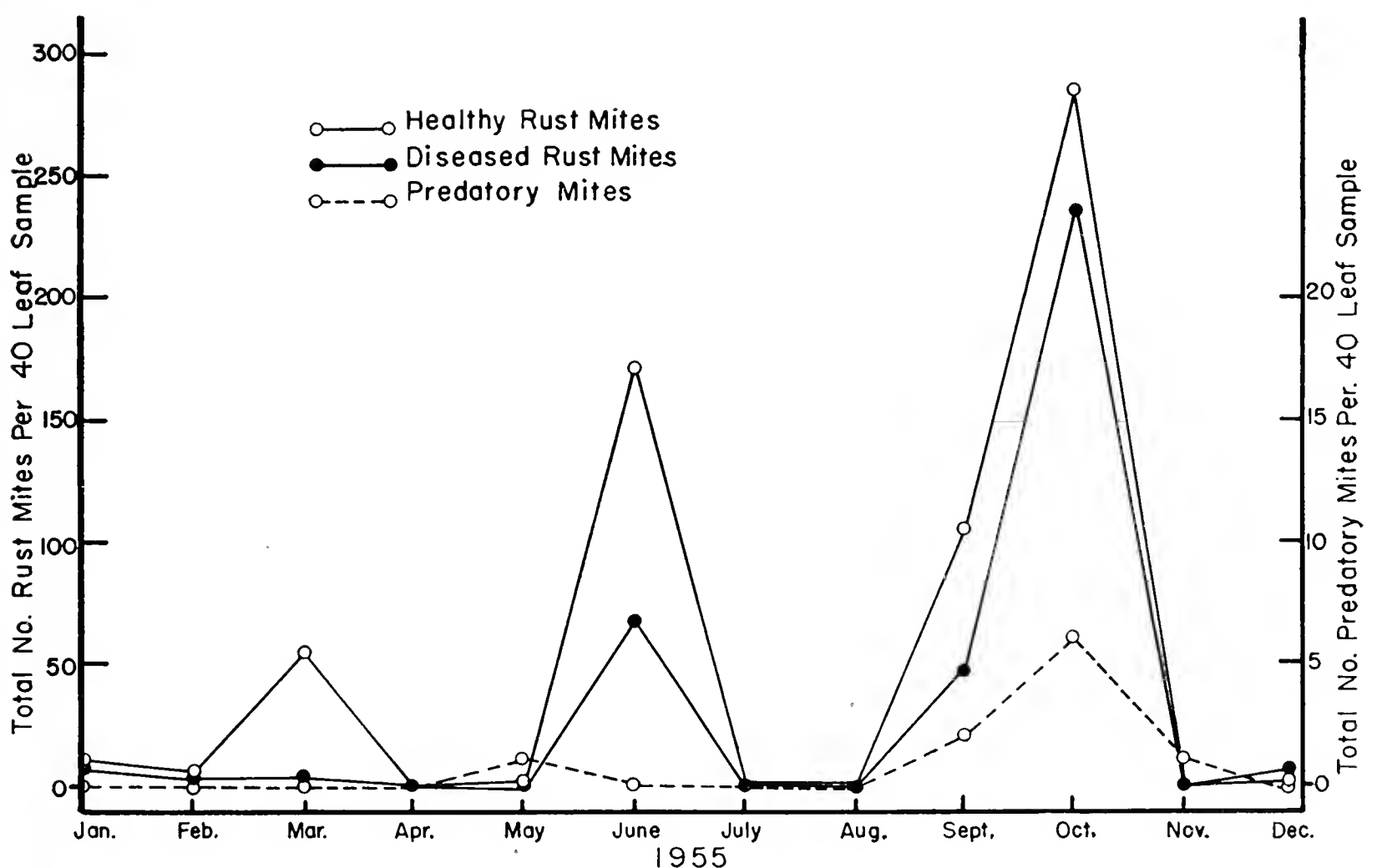


Fig. 2. Comparative populations of healthy and diseased rust mites and predatory phytoseiid mites of the genus *Typhlodromus* from January 1955 to December 1955 in an unsprayed block of Valencia oranges near Twin Lakes in Lake County, Florida.

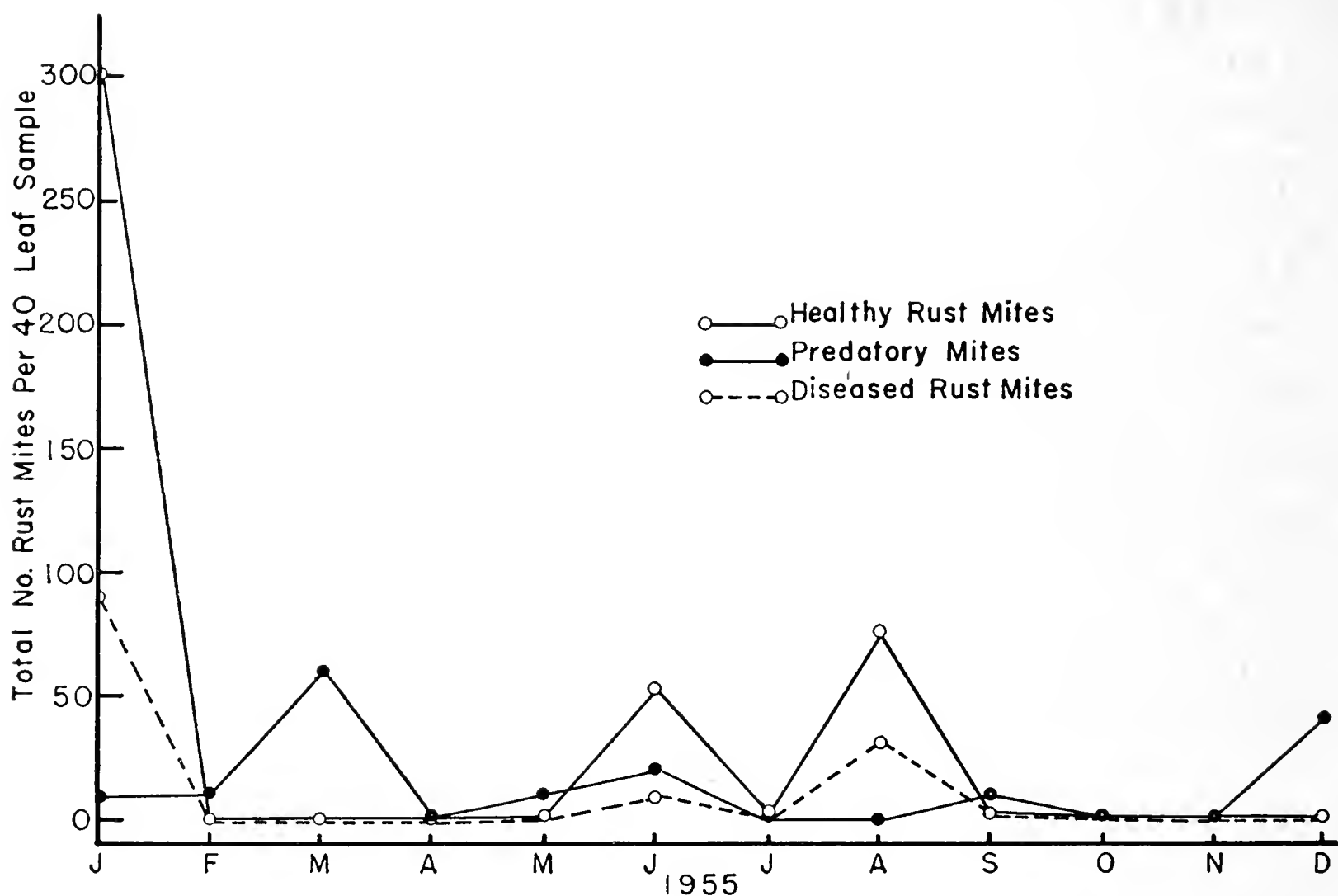


Fig. 3. Comparative populations of healthy and diseased rust mites and predatory phytoseiid mites of the genus *Typhlodromus* from January 1955 to December 1955 in a sprayed block of Valencia oranges near Twin Lakes in Lake County, Florida.

The incidence of *H. thompsonii* is not closely associated with periods of high rainfall and humidity (Figs. 1-3). Although this lack of correlation may again be due to the strong influence of mite density on disease incidence or possibly to a short lived or inefficient infective stage of the fungus, it is probable that some other natural control factor exists in Florida citrus groves.

An intensive search for predators has revealed one common Neuroptera, *C. vicina*, and one uncommon to rare Diptera, *Itonidini*. Several predatory mites in the genera *Typhlodromus*, *Mediolota* and *Pronematus* have been suspect, but to date no feeding has been observed nor consistent statistical correlation obtained. For example, *Typhlodromus peregrinus* Muma is the most common predatory mite in many citrus groves and a negative correlation appears to exist between it and the rust mite during certain seasons and in certain groves, but the correlation is not consistent (Figs. 1-4).

The possibility that temperature and moisture have a direct influence on rust mite populations cannot be overlooked. Such, in fact, could be deduced from the data presented here. In the Fort Pierce grove, high populations of rust mites occurred during July, August, September and October of 1954 and May, June and July of 1955 which were wet months of the respective years (Fig. 1). Further, a winter population of mites occurred in 1955-56, a warm winter, but not in 1954-55, a cold winter.

**CITRUS RED MITE:** The citrus red mite is the most common, widespread and consistently injurious tetranychid found on citrus in Florida. It has been a sporadic problem to citrus growers since the beginning of the century, but in the last 15 years has become of major importance throughout most of the citrus growing areas. During the latter period, several studies have been conducted on this mite. Most of them have dealt principally with chemical control and have included natural control only by inference when treatments resulted in increases in mite populations.

Citrus red mite infestations increase following spray applications containing copper, zinc or sulfur compounds (Thompson 1940 and 1944, Thompson and Griffiths 1950, and Griffiths and Thompson 1950). From this it has been deduced that fungi and possibly predators were being adversely affected by the treatments. The existence of a parasitic fungus of the genus *Entomophthora* causing mortalities as high as 95

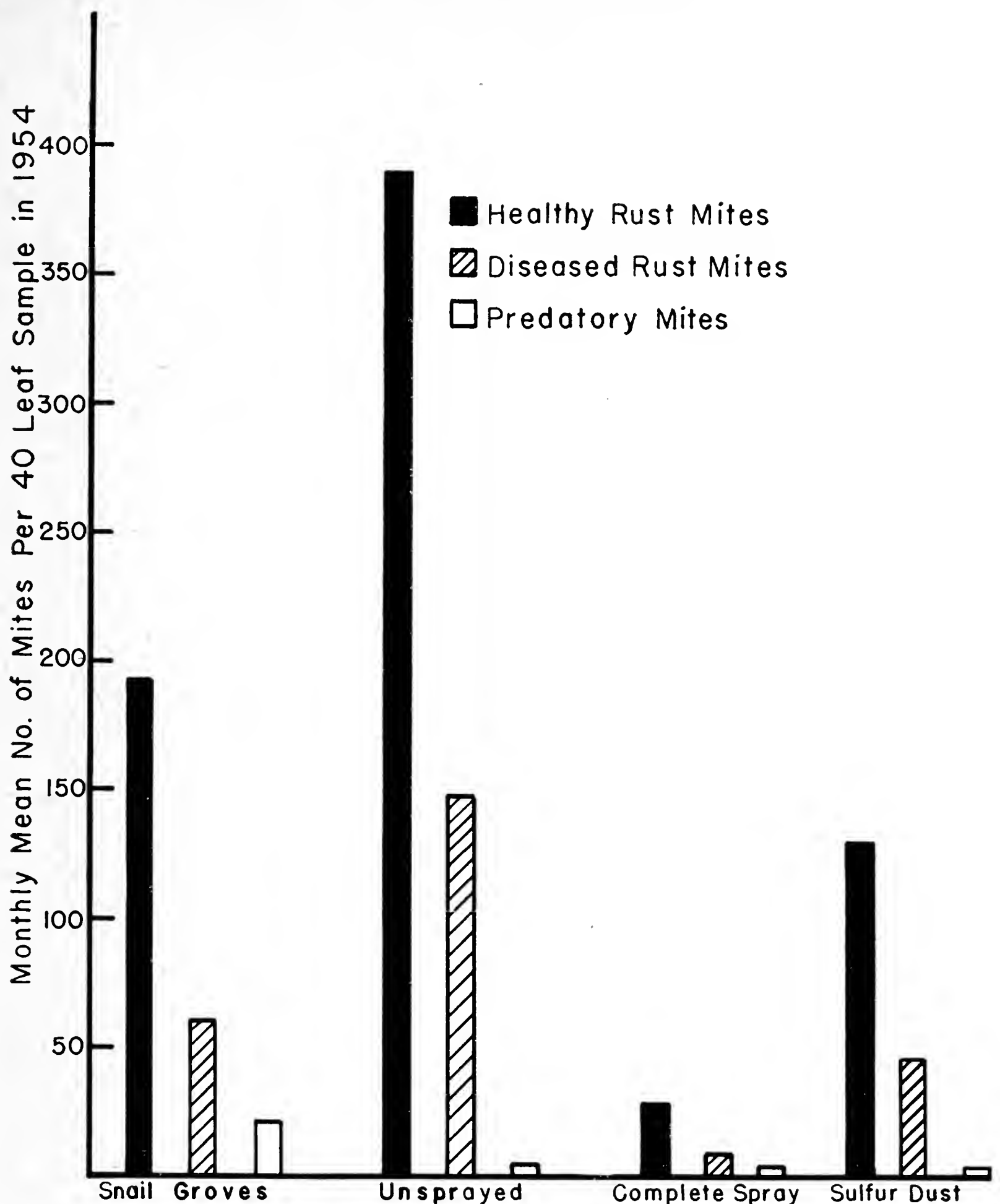


Fig. 4. Mean number of healthy and diseased rust mites and predatory phytoseiid mites of the genus *Typhlodromus* per month in sulfur dusted, complete sprayed, unsprayed and snail groves sampled during 1954.

percent has been proved and reported (Fisher 1951). Recorded mortalities occurred during September and October, complementing observations that citrus red mites disappeared in the summer and early fall (Thompson 1944, and Thompson and Griffiths 1950). Summer mortalities were thought, at one time, to be caused by high temperatures (Thompson 1944), but recent study has shown that an increase in rainfall is followed by "a reduction or at least a leveling off in purple (citrus red) mite activity" (Pratt and Thompson 1953). Repeated observations have demonstrated that spring and summer mite mortalities due to *Entomophthora* range from 30 to over 90 percent and result in population decimation (Muma 1955a).

A second fungus disease of the citrus red mite has recently been discovered and reported to be a species of *Hirsutella* (Fisher 1955). As yet, however, this disease has not been found in other than the one grove.

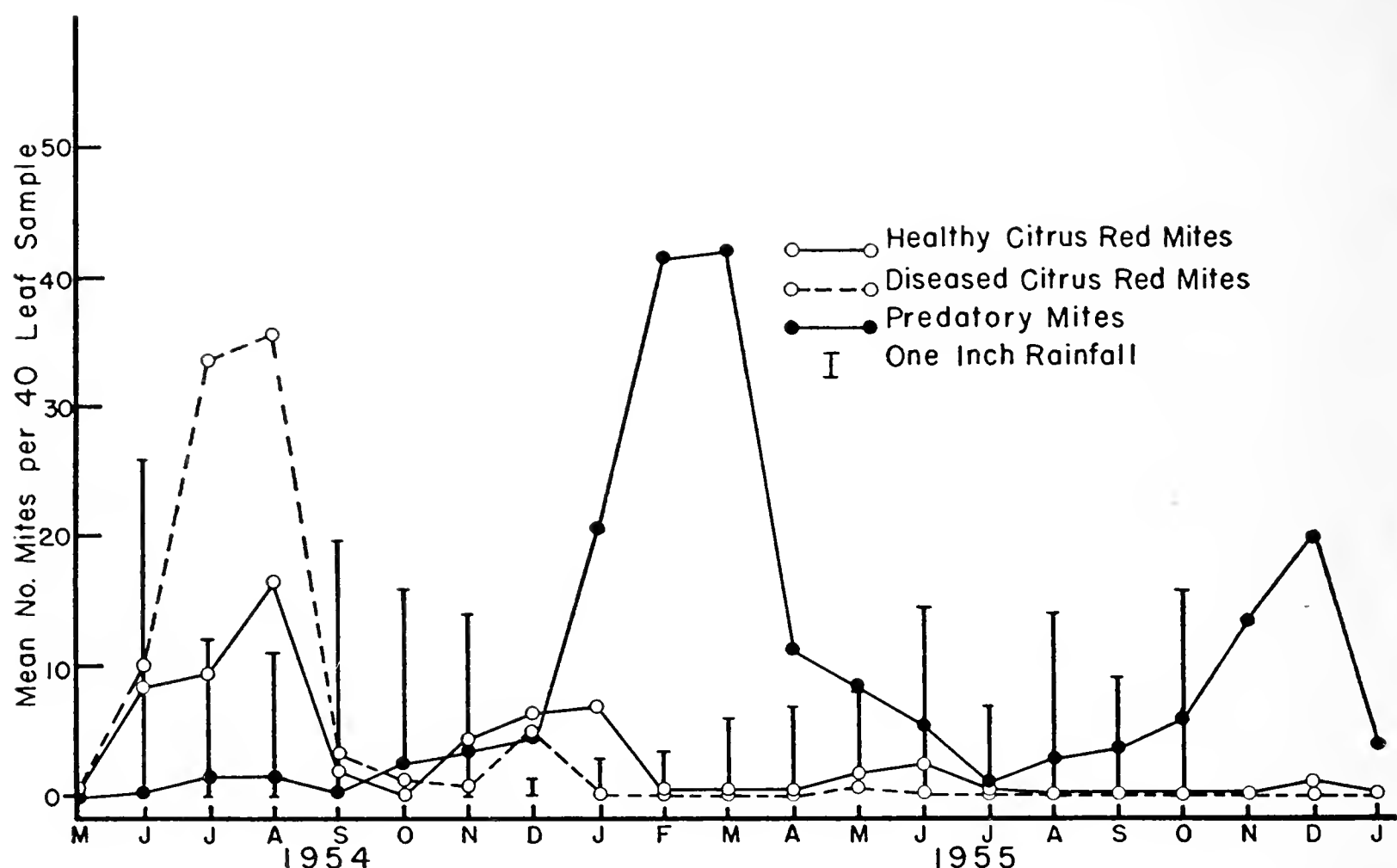


Fig. 5. Comparative populations of healthy and diseased citrus red mites and predatory phytoseiid mites of the genus *Typhlodromus* from May 1954 to January 1956 under varying amounts of rainfall in an unsprayed grove of Valencia oranges at Fort Pierce, Florida.

Few predators of the citrus red mite have been reported from Florida. *Chrysopa lateralis* Guerin, *Chrysopa* sp., *Olla abdominalis* var. *sobrina* Csy. and *Stethorus utilis* Horn have been reported predating on the species, but no correlation has been recorded between predator and host populations (Griffiths and Thompson 1950, and Muma 1955a). *Typhlodromus floridanus* Muma and *T. peregrinus* have been observed feeding on citrus red mites (Muma 1955) and the former has decimated infestations under laboratory conditions (Muma 1955a).

Data obtained during the present study are based on the total number of adult female mites on the 40-leaf-samples. The total number of all diseased stages and total predators were also recorded.

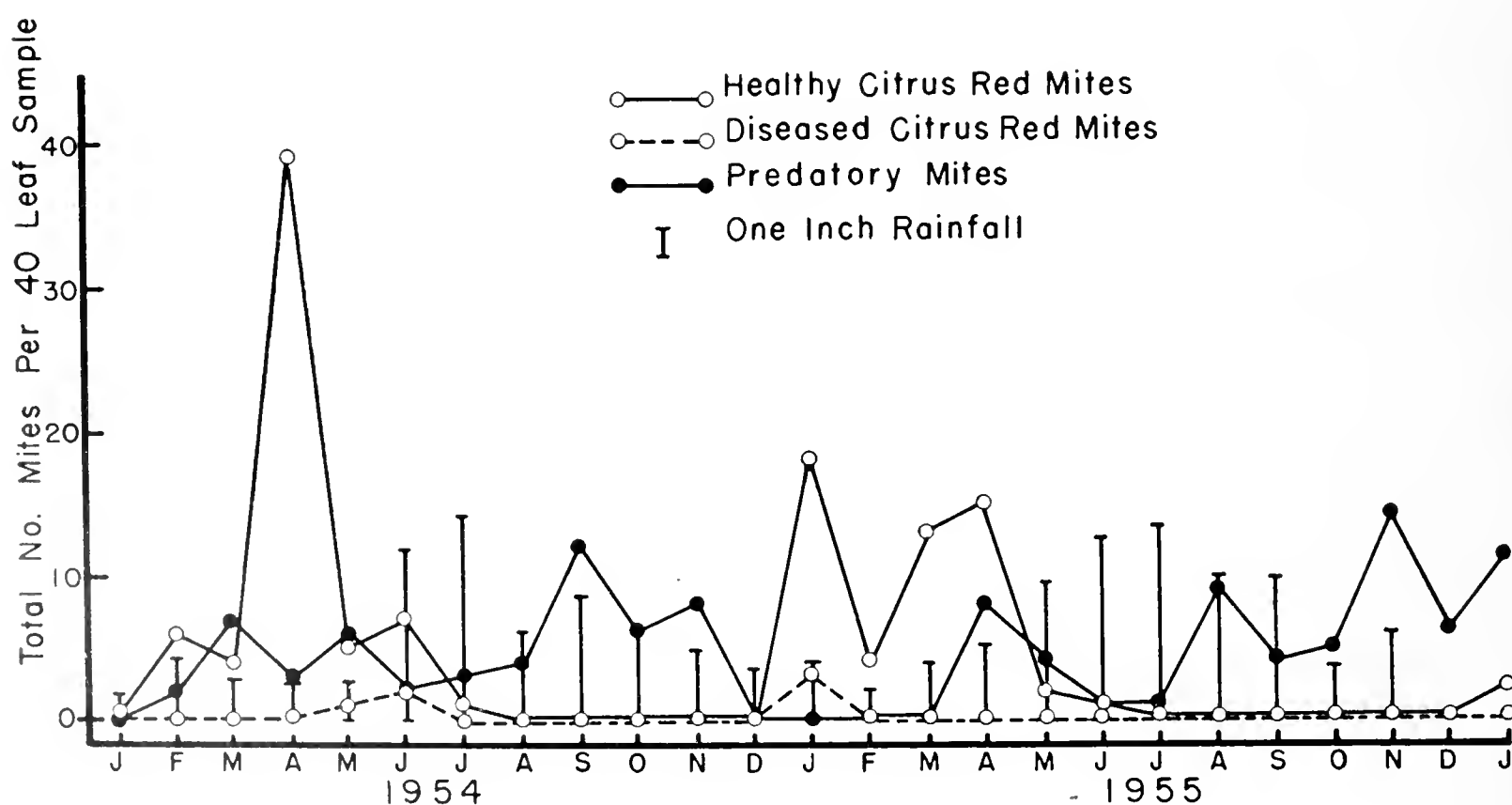


Fig. 6. Comparative populations of healthy and diseased citrus red mites and predatory phytoseiid mites of the genus *Typhlodromus* from January 1954 to January 1956 under varying amounts of rainfall in an unsprayed block of Valencia oranges near Twin Lakes in Lake County, Florida.



Citrus red mites consistently attain population peaks in late winter, spring or early summer with occasional peaks occurring in late fall and early winter. The winter-spring infestations are the heaviest and most prolonged, usually persisting, unless interrupted by spring rains or periods of high humidity, until the beginning of the summer rainy season (Figs. 5-6). Spring, summer and winter increases occurred in the east coast grove (Fig. 5), while the north central grove had the usual winter-spring infestations (Fig. 6).

As has already been demonstrated (Fisher 1951, and Muma 1955a), the virtual disappearance of citrus red mites during rains or periods of high humidity is the result of an increased incidence of *Entomophthora*. Confirming data are found in Figs. 5 and 6 wherein increased rainfall resulted, in most instances, in population decimation following high disease incidence.

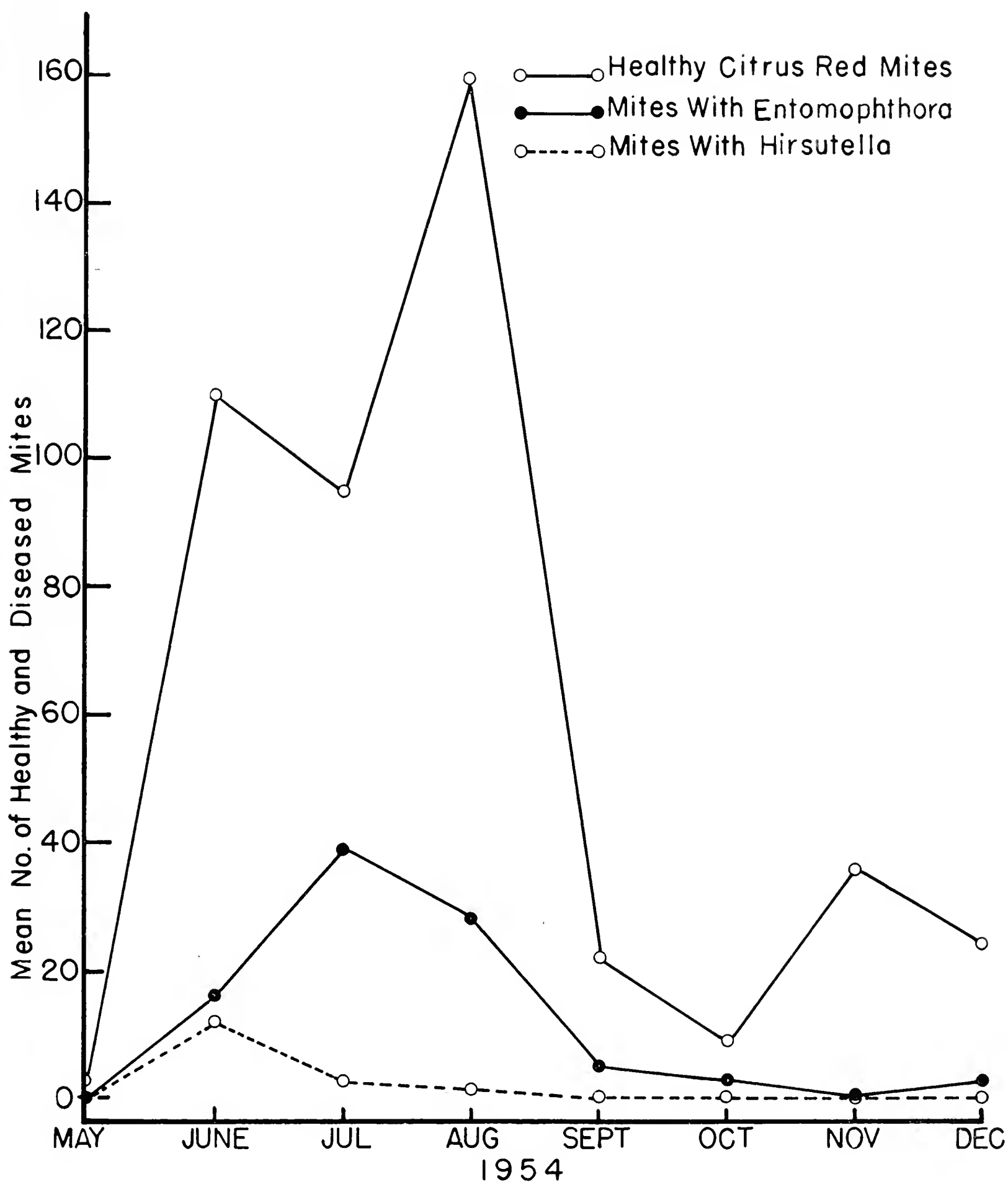


Fig. 7. Comparative populations of healthy, *Hirsutella* infected and *Entomophthora* infected citrus red mites from May 1954 through December 1954 in unsprayed blocks of Valencia oranges at Fort Pierce, Florida.

Fortuitously, the *Hirsutella* reported by Fisher (1955), occurred on citrus red mites in the east coast experimental grove at Fort Pierce, Florida. Although it did not occur in every test block it was sufficiently common in two blocks to be worthy of attention. Observation indicated that *Hirsutella* reached an early peak in the two experimental blocks where it occurred, but did not appear to be as strongly host-density dependent as *Entomophthora* (Fig. 7).

Although data are incomplete at the present time, biological studies on several of the predators reported to have fed on citrus red mites have resulted in some interesting facts. Larger predators, such as *C. lateralis*, *C. interrupta* Schneid and *Olla abdominalis* var. *plagiata* Csy, probably cannot survive on a diet of this mite owing to its small size and non-colonial habits. Such has proved to be the case for *C. lateralis*, as many larvae have failed to survive beyond the second instar in the laboratory even though supplied with abundant mites as food. Smaller predacious species such as *S. utilis*, *T. floridanus* and *T. peregrinus* do survive on a diet of citrus red mites and, when they are present in numbers, may be a factor in natural control. This is particularly indicated for the species of *Typhlodromus* on which some circumstantial evidence has been obtained (Figs. 7-8). Increases in populations of *Typhlodromus* are associated with decreases in citrus red mite populations, except during the late spring and early summer when an undetermined fungus attacks *Typhlodromus* at the same time that *Entomophthora* is decimating citrus red mite populations. The relationship is not statistically significant in all cases, however. In certain groves *Typhlodromus* populations are more closely correlated with numbers of *Hemitarsonemus peregrinus* Beer and *Tydeus* sp., two other mites commonly found on citrus foliage in Florida.

A comparative study of citrus red mite infestations, incidence of *Entomophthora* and *Typhlodromus* populations under different insect control programs indicates a more complex problem than that inferred from past data (Fig. 8). Five groves infested with the snail *Drymaeus dormani* Binney, a fungus-eating arboreal pulmonate, were dusted with sulfur once or twice a year for citrus rust mite control; two groves received sulfur for rust mite control; four groves received nutritional sprays (zinc, manganese and copper), oil or parathion for scale control, and sulfur and DN-111 for mite control; and four groves received no treatments of any kind. Compilation of data from these groves showed that untreated or nearly untreated groves maintained lower red mite infestations than regularly dusted or sprayed groves. As the ratio of healthy to diseased mites did not increase with an increase in density of the citrus red mites, it would seem that the chemical treatments reduce the efficiency of *Entomophthora*, that *Entomophthora* is not host-density dependent, or that some other factor is eliminated by the chemicals. Possibility that the latter inference is correct is indicated by the fact that a negative correlation exists, in the graph, between citrus red mite and *Typhlodromus* populations. However, it is also quite likely that sulfur, copper and possibly other of the spray materials used do have a deleterious effect on the entomogenous fungus, *Entomophthora*, which is offset by a strong influence of host density on disease incidence.

**SIX-SPOTTED MITE:** Although serious infestations by the six-spotted mite are not an annual or widespread problem, this mite must be considered second in importance among the tetranychids in Florida. Past records show that it is a serious problem in one out of every four years (Pratt and Thompson 1953). Despite this fact, however, very few studies dealing with the natural control of the species have been published.

Weather has an important influence on the population intensity of this mite. It has been demonstrated that mite populations are high following cold Decembers and low following warm Decembers and that mite mortalities are high following rains (Pratt and Thompson 1953).

An unidentified disease of six-spotted mites was observed in the spring of 1953 and has been reported (Fisher 1954). Incidence of this disease coincided in time with reported mortalities (Pratt and Thompson 1953), but the disease apparently was not widespread (Muma 1955a).

Predators of six-spotted mites on Florida citrus have been recently surveyed, reported and discussed (Muma 1955, 1955a, 1955b and 1956). Although ten predator

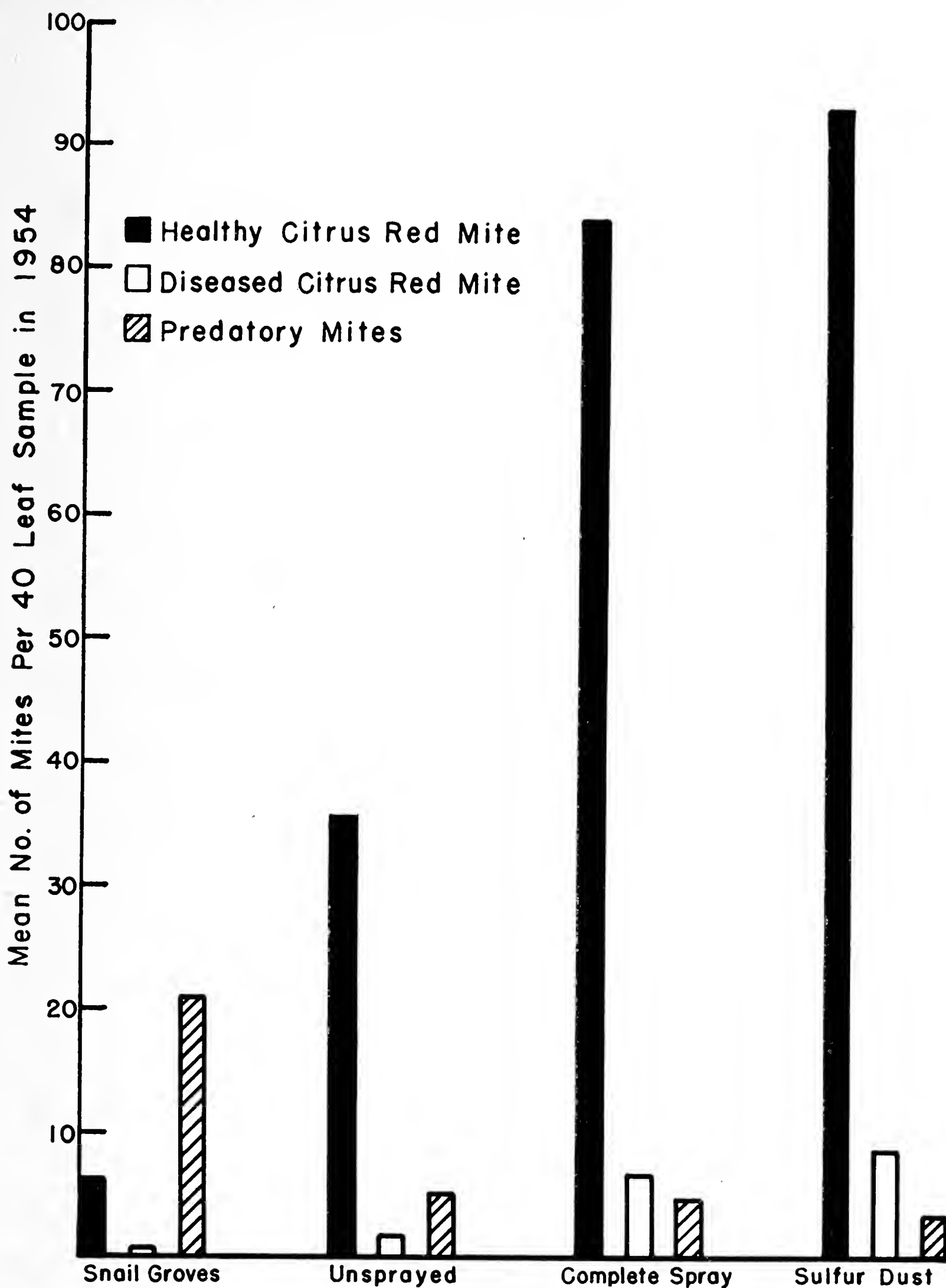


Fig. 8. Mean number of healthy and diseased citrus red mites and predatory phytoseiid mites of the genus *Typhlodromus* per month in sulfur dusted, complete sprayed, unsprayed and snail groves sampled in 1954.

species are known, only three, *T. floridanus*, *S. utilis* and *Scolothrips sexmaculatus* (Perg.), are sufficiently common or consistent to be considered important (Muma 1955a). Of the three, *T. floridanus* seemed to have the greatest influence on the mite populations, with *S. utilis* and *S. sexmaculatus* having respectively less.

The data presented here were obtained from infested leaf samples collected and counted in the same manner as reported by Muma (1955a). Temperature and rainfall data represent three-station means computed from the United States Weather Bureau

monthly reports for Mountain Lake, Winter Haven, and Citrus Experiment Station at Lake Alfred, Florida.

Six-spotted mite infestations attain peaks in March and April of each year and usually decrease to non-economic levels by the middle of May. This population activity has been demonstrated and discussed in several previous reports. The intensity and duration of population peaks are strongly influenced by December temperatures. Heavy prolonged infestations follow cold Decembers whereas lighter infestations of shorter duration follow warm Decembers (Figs. 9-12).

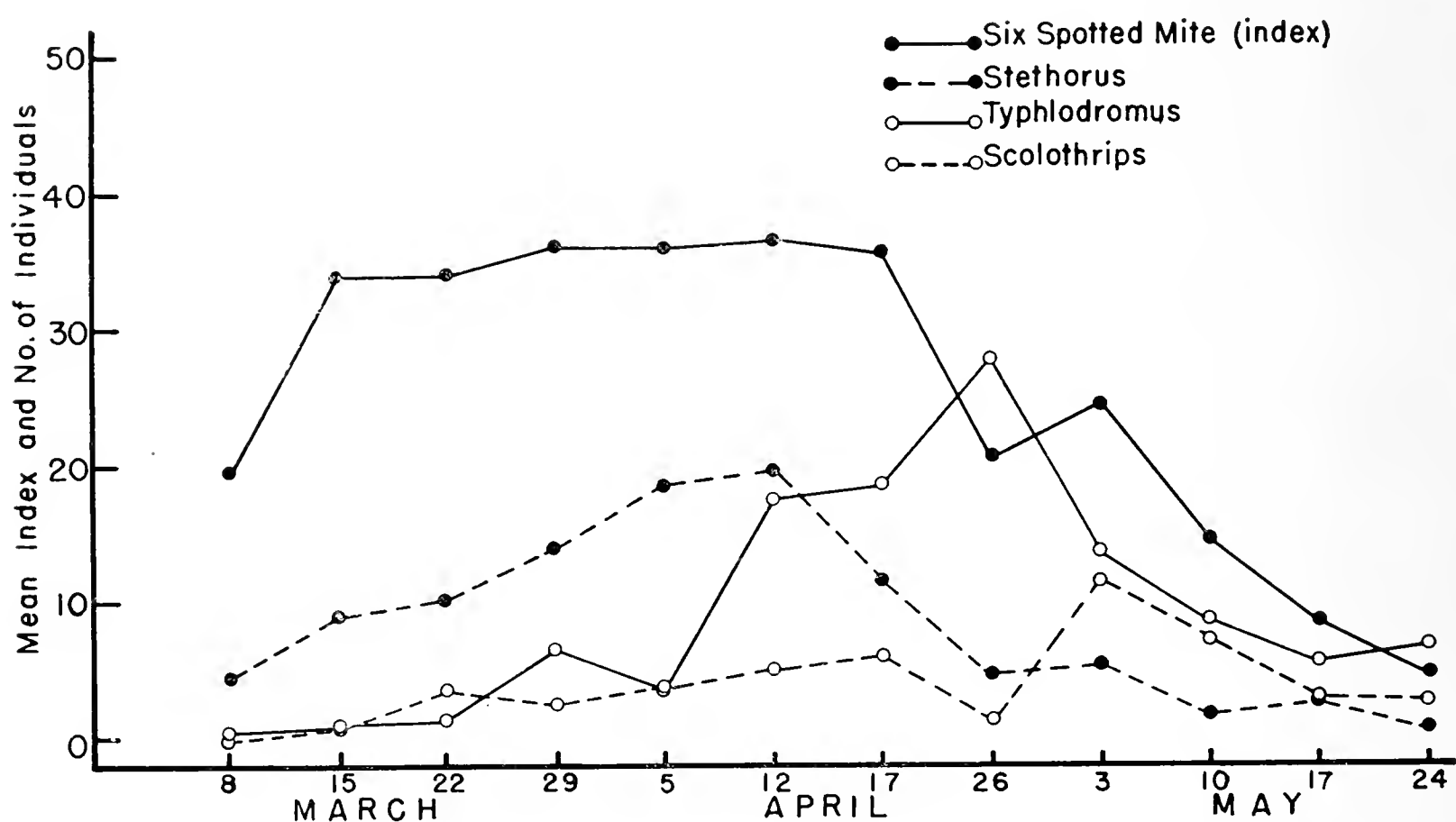


Fig. 9. Comparative populations of six-spotted mites and the three common six-spotted mite predators in eight grapefruit groves from March 8 to May 24, 1955. Polk County, Florida.

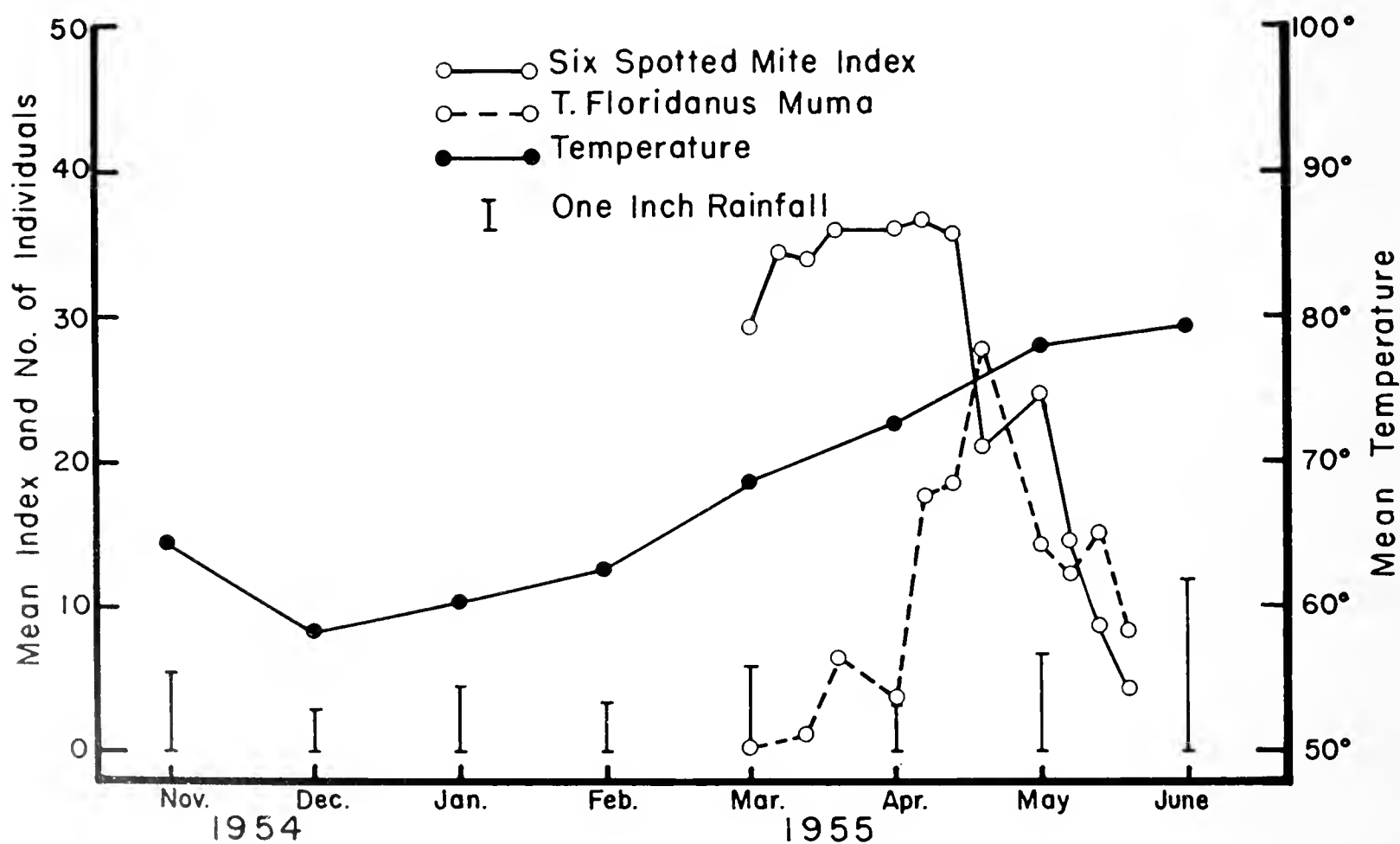


Fig. 10. Mean index of six-spotted mites and number of *T. floridanus* (Muma) in eight grapefruit groves under varying winter and spring temperatures and rainfall in 1954-55. Polk County, Florida.

Population decreases apparently are independent of the intensity of the infestations and may be influenced directly by some physical factor such as temperature or moisture.

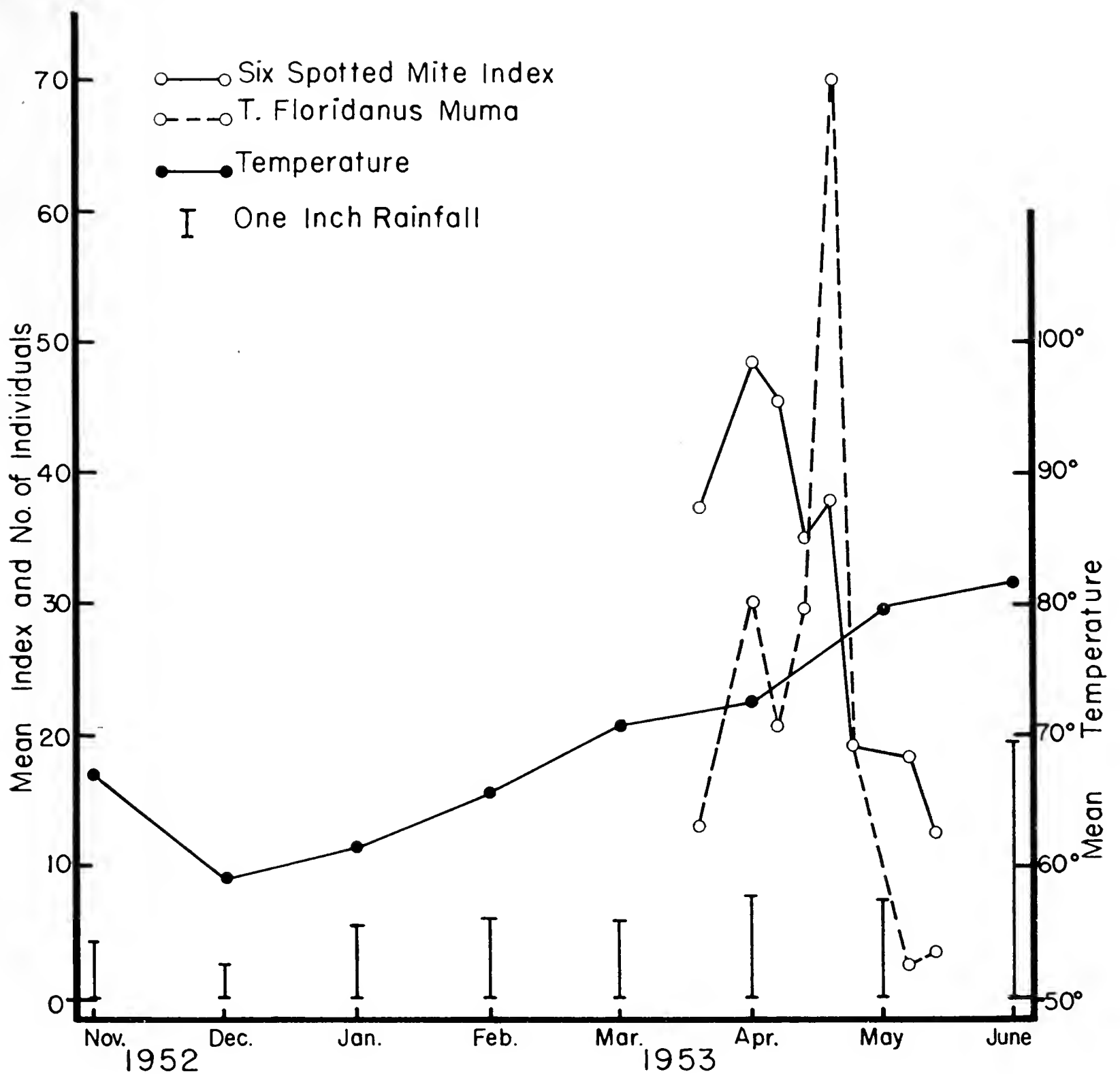


Fig. 11. Mean index of six-spotted mites and number of *T. floridanus* (Muma) in five grapefruit groves under varying winter and spring temperatures and rainfall in 1952-53. Polk County, Florida.

That such may be the case is in fact indicated when increases in mean temperatures are associated with sharp decreases in six-spotted mite populations (Figs. 10-12). A less apparent negative association is also exhibited between populations and total rainfall.

The importance of the biotic factors cannot, however, be overlooked. There is a strong negative relationship between six-spotted mite infestations and populations of *T. floridanus* following warm Decembers (Muma 1955a). A similar relationship is found in data collected following a cold December (Fig. 9). Therefore, it would appear that temperature, rainfall and *T. floridanus* possibly are interacting factors limiting six-spotted mite infestations (Figs. 10-12). Six-spotted mite infestations decreased when the temperature and rainfall increased in April and May. However, the number of *T. floridanus* also increased at the same time. This coincident negative correlation of temperature, rainfall and *T. floridanus* with six-spotted mites makes it impossible to determine, at the present time, which factor or interaction of factors is responsible for the resultant natural control. In addition it should be noted that the spring flush of foliage matures during the same months and that several six-spotted mites containing spherical fungus bodies were collected in the spring of 1955. The latter two factors may also play a part in the control obtained in certain groves.

**TEXAS CITRUS MITE:** This spider mite has only recently been discovered attacking citrus in Florida. The first specimens were collected in the northern part of the east coast citrus area in 1951 and have been recorded and discussed (Muma *et al.* 1953).



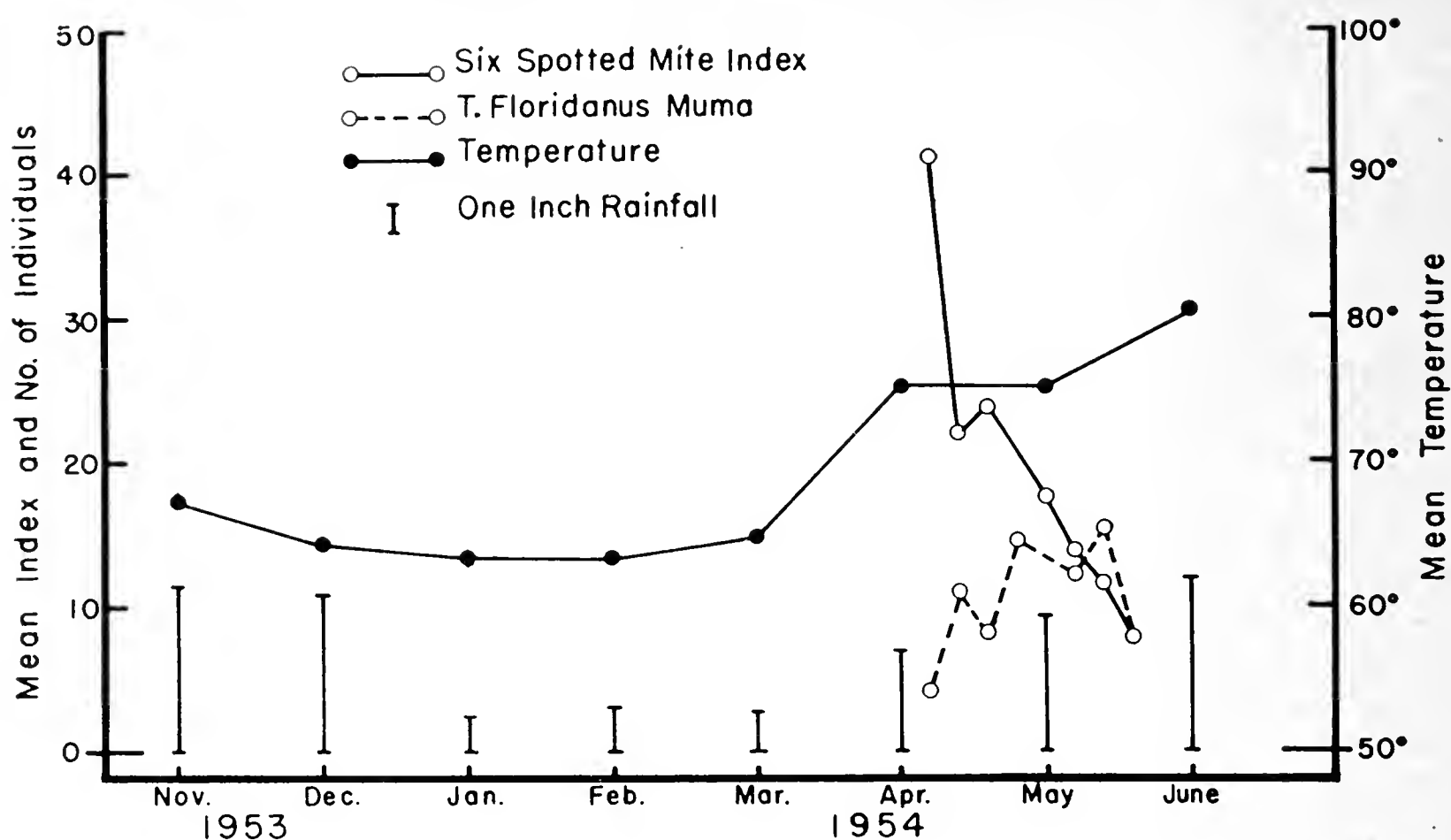


Fig. 12. Mean index of six-spotted mites and number of *T. floridanus* (Muma) in nine grapefruit groves under varying winter and spring temperatures and rainfall in 1953-54. Polk County, Florida.

Since that time the range of the species has been extended westward and southward (Muma 1954 and 1955c). It is possible that the species, as it spreads through the citrus areas of the state, will become of economic importance.

An undescribed species of *Entomophthora* has been reported to attack this mite (Fisher 1954). *T. floridanus* has also been shown to feed on the species (Muma 1955). No other notes dealing with the biological control of this mite in Florida have been published.

Data obtained during the present study are based on the total number of adult female Texas citrus mites and total number of predators on a 40 leaf sample.

Although fluctuations of the populations of this spider mite have been studied in only two groves, they appear to be the same as those of the citrus red mite. Peaks of infestation are usual in the late winter, spring and early summer with the lowest populations occurring in the late summer and early fall. This fluctuation strongly indicates the existence of a fungus disease similar to that known to control citrus red mites. Such a disease has been reported (Fisher 1954), and population decreases in the summer rainy season and humid winter months (Fig. 13) add strong circumstantial evidence to the thesis. It should be further noted that populations of *Typhlodromus* spp., the only known predators of the mite in the state, have no consistent relationship to populations of the host mite.

**FALSE SPIDER MITE:** This phytophagous mite is widely distributed, common and sometimes abundant in unsprayed citrus groves in the state. Although easily controlled by sulfur or DN compounds (Knorr and Thompson 1954), it can and occasionally does become a problem in natural or biological control groves. With the exception of taxonomic references, little has been published on this mite under Florida conditions. The species has been recorded as abundant and injurious in a nursery of Temple orange, grapefruit and sour orange trees at Orlando, Florida in July 1948 (Baker 1949). Also included in this report were notes by R. L. Miller on the type of damage and egg deposition.

The data presented here are based on the total number of mites and predators on 40 leaf samples.

Infestations of the false spider mite attain peaks of population in the summer and early fall (Fig. 14). Lowest infestation occurs during the winter and early spring. Intensive study has failed to reveal a fungus attacking this mite and such can be

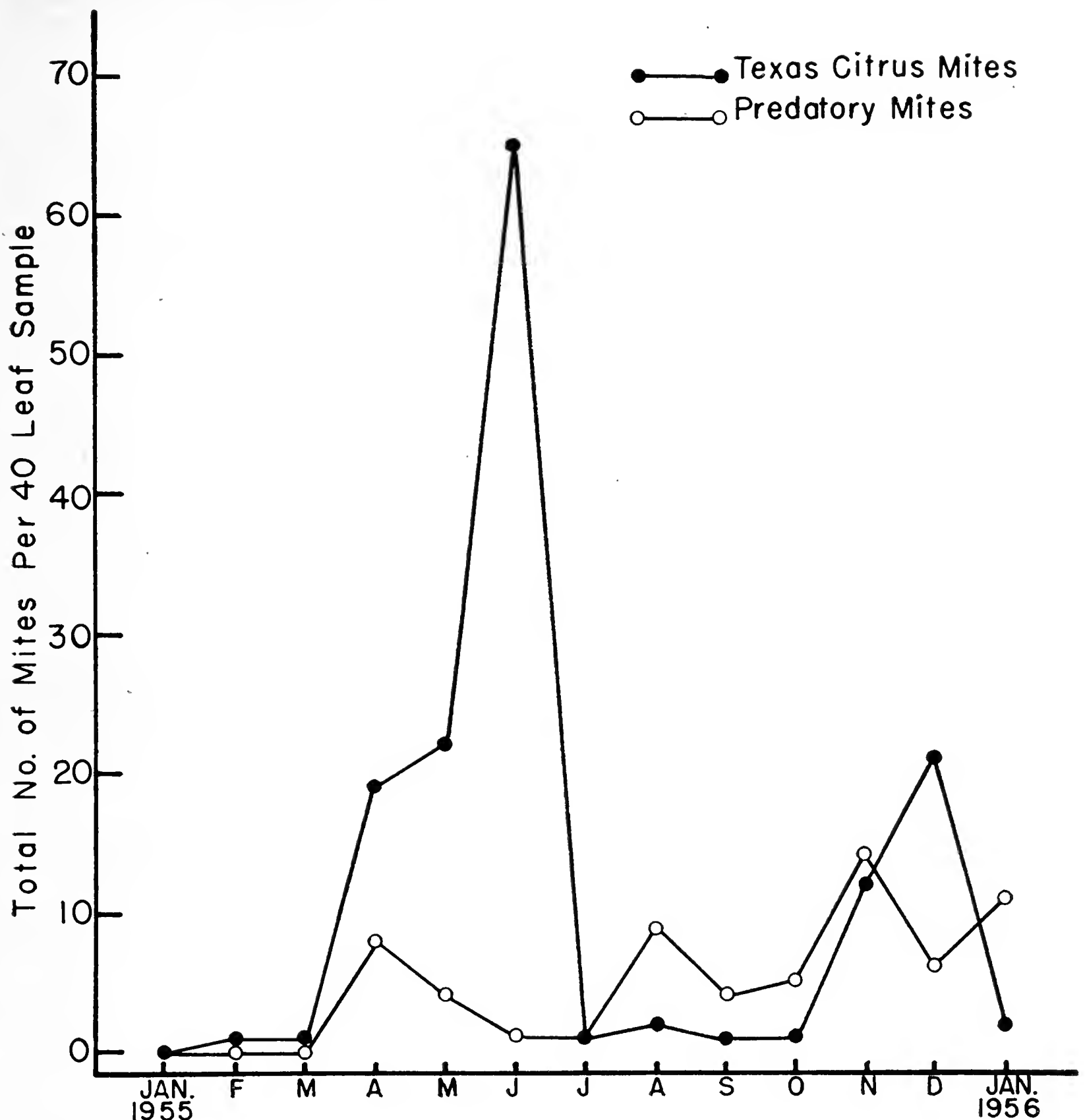


Fig. 13. Comparative populations of Texas citrus mites and predatory phytoseiid mites of the genus *Typhlodromus* in an unsprayed block of Valencia oranges near Twin Lakes in Lake County, Florida during 1955.

interpreted from the data, as fungi normally cause epizootics during the warm, wet summer and early fall. As yet no predator has been observed feeding on this species. There was, however, a strong negative correlation between a population complex of *Typhlodromus* and *Amblyseius* and the summer-fall infestation of the false-spider mite in the grove (Fig. 14).

### SUMMARY AND CONCLUSIONS

An attempt has been made to compare, integrate and evaluate published and unpublished data on the natural control of the five most common and widespread phytophagous mites found on Florida citrus. They are the citrus rust mite, citrus red mite, six-spotted mite, Texas citrus mite and false-spider mite.

Citrus rust mite infestations are reduced during the late summer and early fall by the high incidence of an entomogenous fungus that is associated, if not identical, with *Hirsutella thompsonii* Fisher. The greater the mite density, the greater is the degree and duration of such reduction. Mite populations also seem to be directly influenced by temperature and moisture. However, the part played by weather in the natural control of the species has not been adequately proved nor is it fully understood.

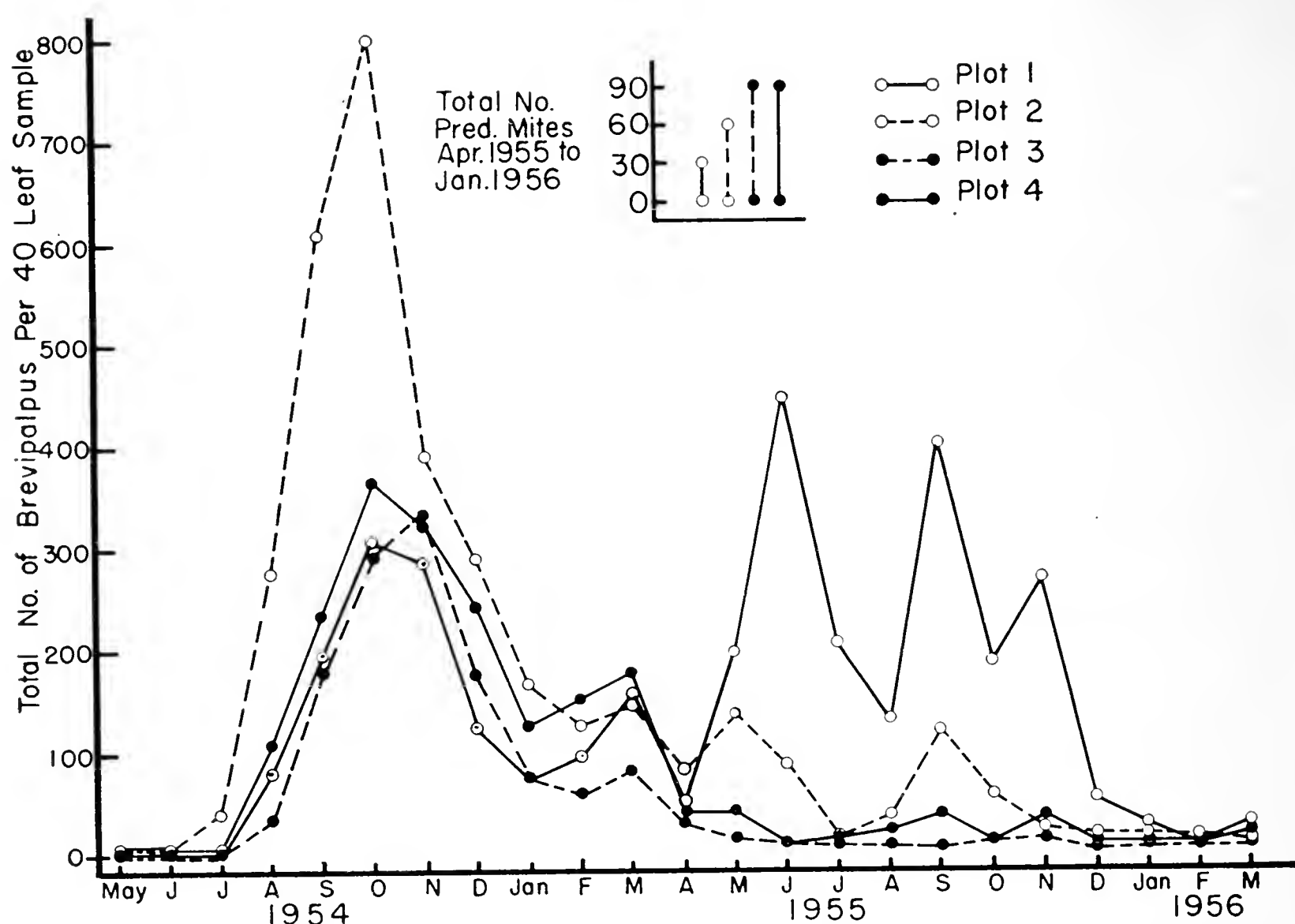


Fig. 14. Populations of false spider mites, *Brevipalpus phoenecis* (Geijskes), from May 1954 to February 1956 and numbers of predatory phytoseiids of the genus *Typhlodromus* from April 1955 to January 1956 in several experimental plots of Valencia oranges at Fort Pierce, Florida.

To date no known predator has been demonstrated to reduce rust mite infestations, but the existence of such is indicated in the quick recovery and high incidence of mite infestations following the application of certain insecticides.

Citrus red mite infestations are controlled during periods of high humidity or rainfall by the entomogenous fungus, *Entomophthora* sp. The degree and extent of such control appears to be strongly host-density dependent. Also there is evidence that certain increases in citrus red mite infestations following applications of insecticides and acaricides are at least partly the result of mortalities among predatory phytoseiid mites. On the other hand, it is felt that large predators do not play a major role in the natural control of this mite owing to its small size and inadequacy as food for such predators. A second, as yet little known, fungus, *Hirsutella* sp., has recently been found to attack this mite.

Six-spotted mite infestations vary from year to year in intensity and duration. This variation has been correlated with temperatures during the preceding December; low temperatures produce heavier, more prolonged spring infestations than high temperatures. Predator populations, particularly those of *Typhlodromus floricola* Muma, seem to reduce the mite populations to non-economic levels about the middle of May each year. This reduction appears to be independent of December temperatures and intensity of mite infestation, but apparently is related to high spring temperatures and increased rainfall. Although a fungus disease is known to exist, it has not in recent years been sufficiently common to evaluate.

Texas citrus mite infestations are controlled during the wet summer months by some natural control agency. It is felt that this agency is probably a species of *Entomophthora* that is known to attack this mite.

False spider mite infestations are subject to cyclic periods of high and low intensity. As decreases in infestations do not occur during periods of high humidity or rainfall, predators rather than disease are suspect. A complex of predatory phytoseiids seems, at present, to be the cause of such decreases.

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# On the Ecology of Typhlodromid Mites in Southeastern England<sup>1</sup>

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## ABSTRACT

*Predacious typhlodromid mites are widely distributed in southeastern England. However, only Typhlodromus tiliae Oudemans is abundant in commercial orchards. Many aspects of the life-history and ecology of this species have been studied but only those related to its interactions with Metatetranychus ulmi (Koch), the European red mite, are reported here. These involved an investigation of the distribution of the predator and its prey on fruit trees, and it is shown that the former is independent of the latter, as the two species inhabit different locations. This renders T. tiliae relatively ineffective as a predator of M. ulmi; this conclusion is supported by the results of a field experiment designed to avoid the complicating factors inherent in the use of chemicals to achieve predator gradients.*

*Brief reference is made to other aspects of the ecology of the predator, all adding to the picture of a species that does not possess the attributes desirable in an economically important predator.*

## INTRODUCTION

Interest in the possibility of using biological means for the control of orchard-inhabiting phytophagous mites in Western Canada has increased in recent years, and in 1951 a research project on this subject was initiated jointly by the Fruit Insect and Biological Control Units of the Entomology Division. Emphasis was placed on predacious mites because these were generally believed to be among the most important predators of these pests.

Previous knowledge concerning orchard-inhabiting predacious mites, mainly "typhlodromid" mites of the genera *Typhlodromus* Scheuten, *Amblyseius* Berlese, and *Phytoseius* Ribaga was slight, and was much less than was needed if they are to be used intelligently for biological control in orchards. Much could be learned from English workers in this regard, and in 1952 the author was temporarily transferred to England. The scope of the project was widened at this time to include all phases of the biology and ecology of typhlodromid mites in southeastern England, not merely their place in orchard economy.

Intensive study soon revealed that these mites are not as effective predators of phytophagous mites within the study area as was generally believed. The reasons for their failure to control harmful species satisfactorily were investigated and the present paper is a report of this aspect of the investigation.

The effects of predacious mites were investigated in the past by field experimentation involving the use of chemicals to obtain differential populations of the predators. Inverse numerical relationships between predators and prey were usually taken as proof that the predator was effective. This, however, is only the first step when attempting to demonstrate the effectiveness of any predator and does not constitute proof; it merely suggests that the predator may be a factor that influences prey density. A second step to definitely establish the dependency of such a relationship, is necessary in every case. The danger of accepting an inverse numerical relationship without further evidence lies in the fact that one can never be sure that the relationship is casual; it may be the result of the two organisms each reacting in different ways to a complex of environmental factors.

Not everyone will agree that such relationships obtained by chemical means do not constitute proof of predator value. However, aside from the fact that in most field experiments that involve predacious mites, predacious insect populations were not recorded and thus their effects were apparently not considered, the literature contains several references to the possibility of unknown side-effects that may follow the use of chemicals and that render field results useless or actually misleading. For example,

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several insecticides toxic to predators are suspected to cause increases in phytophagous mite populations by physical or physiological means (Hueck *et al.*, 1952). Regardless of whether or not the data that have been advanced to support these views are accepted, the suspicion that such might be the case renders the use of these chemicals inadvisable for predator studies, and yet these are the chemicals used most frequently.

Because such methods are suspect, an attempt was made during the present investigation to gain an understanding of the mode of action of predacious mites from detailed biological and ecological studies. The resulting conclusions were tested in the field by means of a trial not dependent on chemicals to obtain predator differentials.

## RESULTS

Details of the life-histories and feeding habits of the typhlodromids studied will be presented elsewhere, but one aspect of their feeding bears directly on their effectiveness as predators. These mites can live for a considerable time on apple leaves without other food, and can develop and oviposit in an apparently normal fashion when provided only with fungal spores or plant pollen; prey in the form of other mites is not necessary to their survival and development, and therefore it was necessary to investigate the role played by alternative foods, such as spores and pollen, in the field.

When typhlodromids feed upon tetranychid mites their intestines assume the colour of the prey and this shows through the transparent body wall. The colour is reddish when the European red mite is the prey, and experimentation showed that this persists for three days in most individuals, gradually fading to brown. This constitutes therefore, a convenient index which can be used in the field to determine which individuals have preyed recently on the red mite; colourless individuals may be considered not to have fed upon this prey for three days or more. In England, it was usually found that not more than from 40 to 50 per cent of the predacious mite population in orchards and on trees, where the red mite was abundant, had recently fed on this prey, and it was concluded that alternative sources of food were utilized to a considerable extent by wild populations. The percentages of individuals that had fed recently on red mites remained relatively constant throughout the season despite a tremendous increase in prey density, indicating that this low incidence of predation was not a consequence of the unavailability of prey.

When these facts had been established, the study was continued to determine if there were reasons for this in addition to a natural disinclination to feed exclusively on the red mite. This involved an investigation of the population characteristics of typhlodromids and of their prey.

Emphasis is placed on *Typhlodromus tiliae* Oudemans in the following discussion because it is the most common species in cultivated orchards in southeastern England, and therefore it is the only species at present that can be considered economically important. For the same reason, emphasis is also placed on *Metatetranychus ulmi* (Koch), the European red mite.

### DISTRIBUTION OF PREDATORS AND PREY ON APPLE TREES

The distribution of a predator within its environment is a population characteristic that may influence its effect on its prey. For a predator to exert its maximum effect it should be present and active in all places inhabited by the prey. A predator may not be able to effect permanent control of a pest if there are areas where the pest is free from attack as continual reinfestation will occur from these areas to the detriment of any balance the predator may have been able to achieve.

The ultimate habitats of predacious mites on fruit trees are individual leaves, and the distribution on these may be important. Also of possible interest may be their distribution on units of several leaves, namely spurs and shoots. Their distribution in these places should reflect a response to environmental influences such as microclimate and the physical characteristics of the host plant. This, however, does not necessarily apply to their distribution within the tree itself; other factors may exercise disturbing influences, such as the site of overwintering quarters, and this aspect of distribution was not studied.

In addition to spatial distribution, numerical variation between habitats is also worthy of study as this also may reflect population character. In the present study an investigation of the distribution of *T. tiliae* and *M. ulmi* on leaves, between leaves, and along shoots and spurs was undertaken to gain a more complete understanding of the effectiveness of the predator, and of its limitations.

The distribution of predacious mites was studied in derelict orchards and that of *M. ulmi* in a commercial orchard where predators were absent and where there was no possibility that prey distribution had been modified by the action of predators. It was impossible to demonstrate the effect of the predator on the distribution of prey because commercial orchards where both were abundant were not available for investigation.

In 1954 and 1955 the mites on the lower surfaces of leaves collected at regular intervals were counted immediately after collection and their positions plotted on a stylized plan. The composite plans obtained are shown in Fig. 1. Of the predators, *T. finlandicus* Oudemans (A) (a species abundant in derelict orchards) showed no preference for any part of a leaf and was uniformly distributed over the lower surface. On the other hand, *T. tiliae* (B) was found only along the central rib and larger subsidiary veins. Like *T. finlandicus*, *M. ulmi* (C) was distributed uniformly, though early in summer concentrations sometimes occurred along the midrib. These patterns were observed on many varieties of apple, and factors such as leaf pubescence and size seemed to have little influence on them.

Because of these distribution patterns on individual leaves, a large proportion of the *M. ulmi* population is relatively free from attack by *T. tiliae*. It is true that *M. ulmi* adults wander freely over the leaf and those that cross the midrib are vulnerable to attack. However, adults not destroyed in this manner (and laboratory experiments suggested that adult stages are the least favoured mite foods of typhlodromids) are free to lay eggs with impunity on much of the leaf surface. *T. finlandicus* is rarely found under commercial conditions, but because its distribution is similar to that of *M. ulmi* it is potentially a more effective predator than is *T. tiliae*.

The leaf plans in Fig. 1 show only the lower surfaces of apple leaves. Phytoseiids rarely are found on the upper surfaces in the field, but from 15 to 30 per cent of the total *M. ulmi* population, even at low densities, is located here (Blair and Groves, 1952). This proportion is free from attack by phytoseiids and, therefore, perhaps neither *T. tiliae* nor *T. finlandicus* can be completely adequate as a control agent.

#### INTERLEAF DISTRIBUTION OF PREDATORS AND PREY

To follow the development of *T. tiliae*, frequent collections of leaves were taken from the derelict orchard in 1955. To investigate the interleaf distribution of this mite, records were taken of the numbers on individual leaves, as well as of the total population, from May to mid-September. These were divided into those taken in early summer (May-June), mid-summer (late June, July, early August), and late summer (late August, early September).

Negative binomial distributions were fitted to these three populations of *T. tiliae*. The fit was excellent in early summer, good in mid-summer and poor in late summer and early autumn. In the last case higher numbers were observed than one would expect from the negative binomial distribution; presumably there were disturbances that influenced the population other than those caused simply by movement of the mites. These may have been leaf senescence, predation by insects, or a number of other factors not investigated. Changes in the parameters of distribution, the mean and the exponent, indicated increased dispersion during the season as well as an increase in total numbers.

Data on the interleaf distribution of *T. tiliae* are shown in Fig. 2, and then biological significance clearly indicated. In early and mid-summer most of the population was concentrated on a few leaves. Probably these were colonized by overwintered females that produced progeny which did not disperse generally until late summer and early autumn. Therefore for much of the year there were many leaves on which no, or very few, predators were present. This investigation was conducted on a site where the numbers of *T. tiliae* were greater than those usually found in commercial orchards.

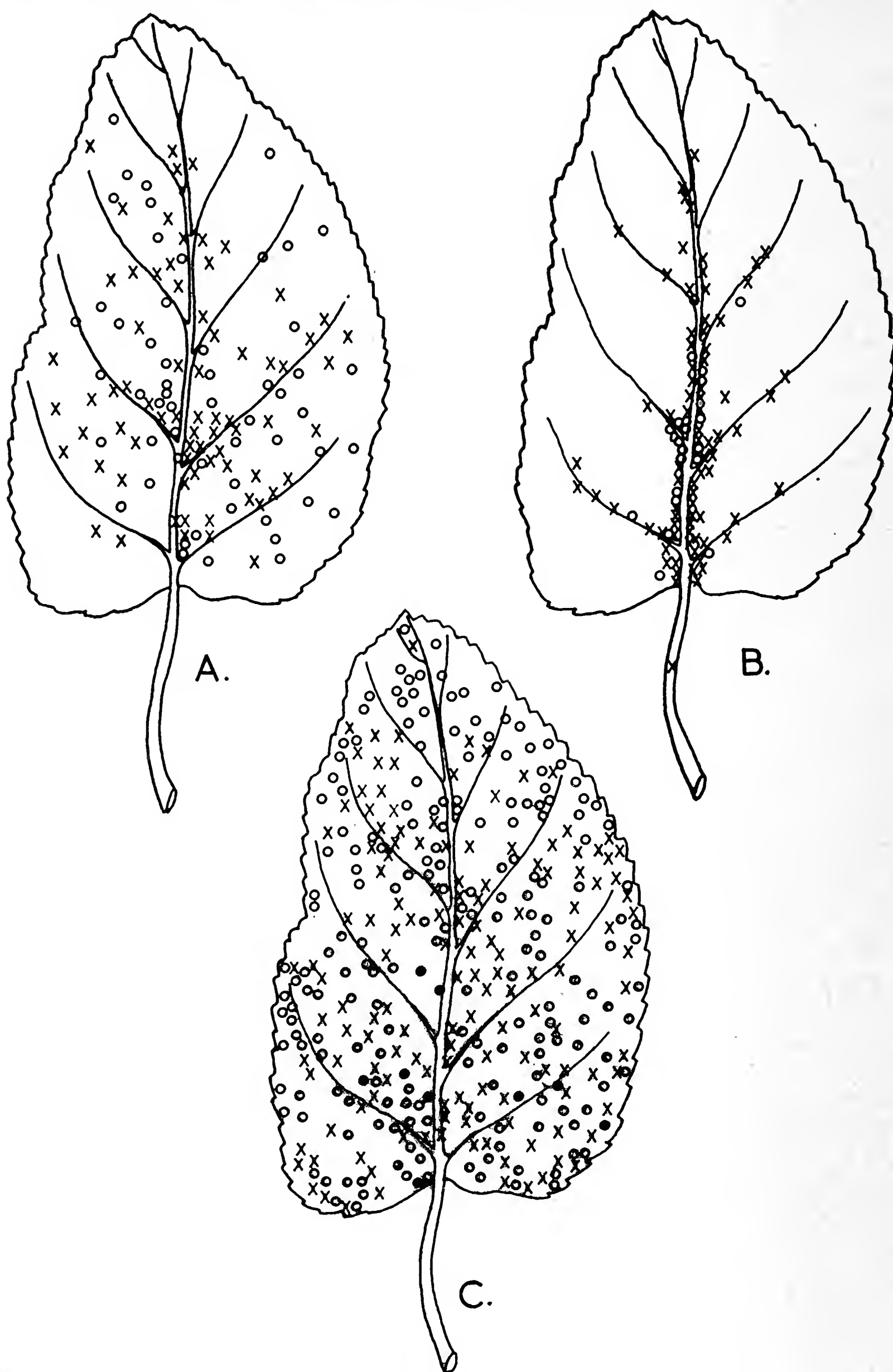
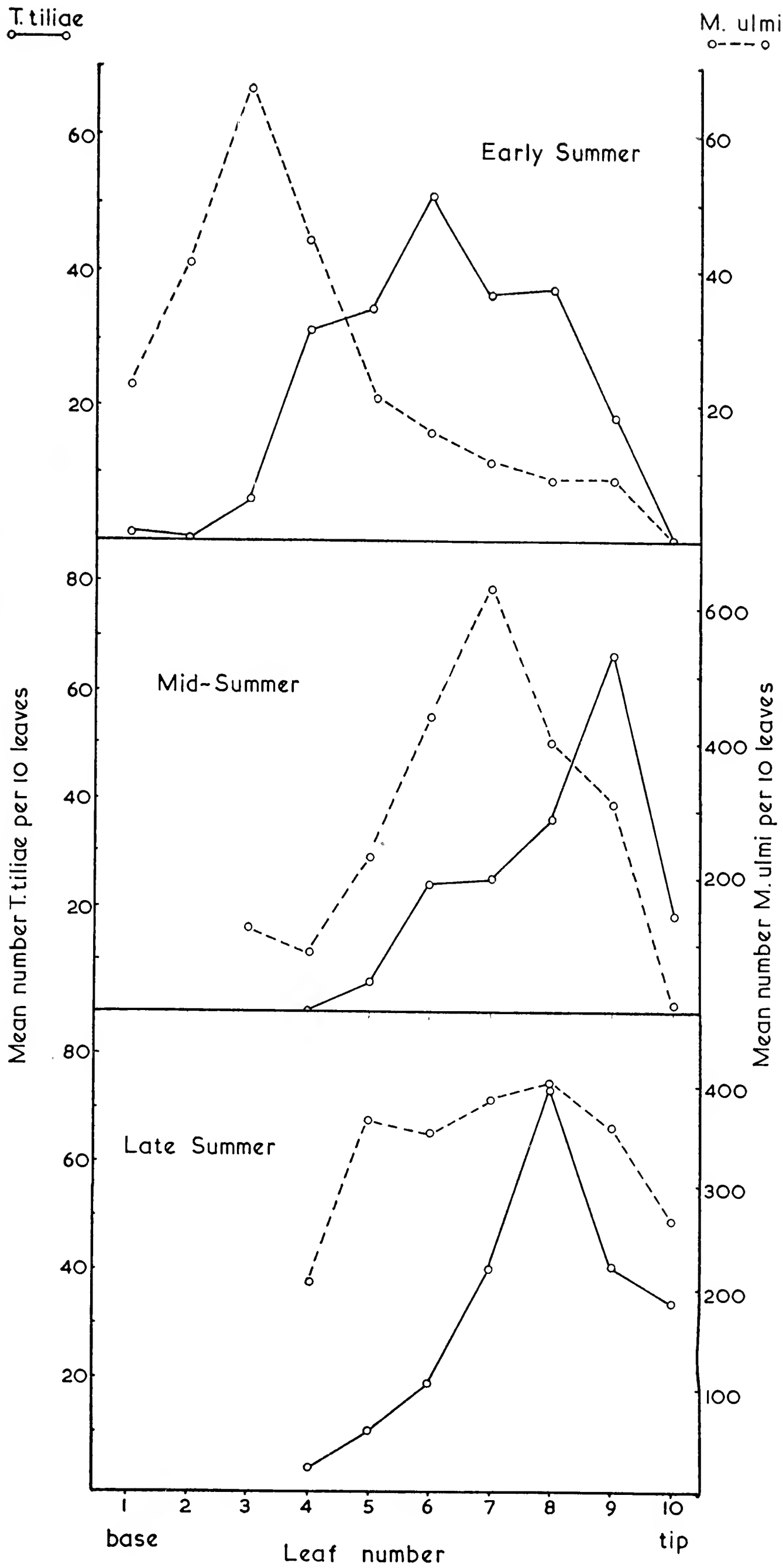


Fig. 1. Distribution on the lower surfaces of apple leaves (composite diagram):  
 A, *Typhlodromus finlandicus* Oudemans;  
 B, *Typhlodromus tiliae* Oudemans;  
 C, *Metatetranychus ulmi* (Koch).

Fig. 2. The interleaf distribution of *Typhlodromus tiliae* Oudemans, 1954 and 1955.





A similar study was conducted in 1954 and 1955 on the distribution of *M. ulmi* between leaves. A negative binomial distribution was fitted to the population observed in May-June but it was not a good fit; there were fewer leaves with no mites and more with small numbers than would be expected on the negative binomial hypothesis. This suggested a more even distribution of *M. ulmi* over the leaves, with however, some large clusters. Whatever the cause, the distribution was quite unlike any observed for *T. tiliae*, as shown in Fig. 3, and it is unlikely that a predator distributed as *T. tiliae* could be fully effective against a prey distributed as *M. ulmi*.

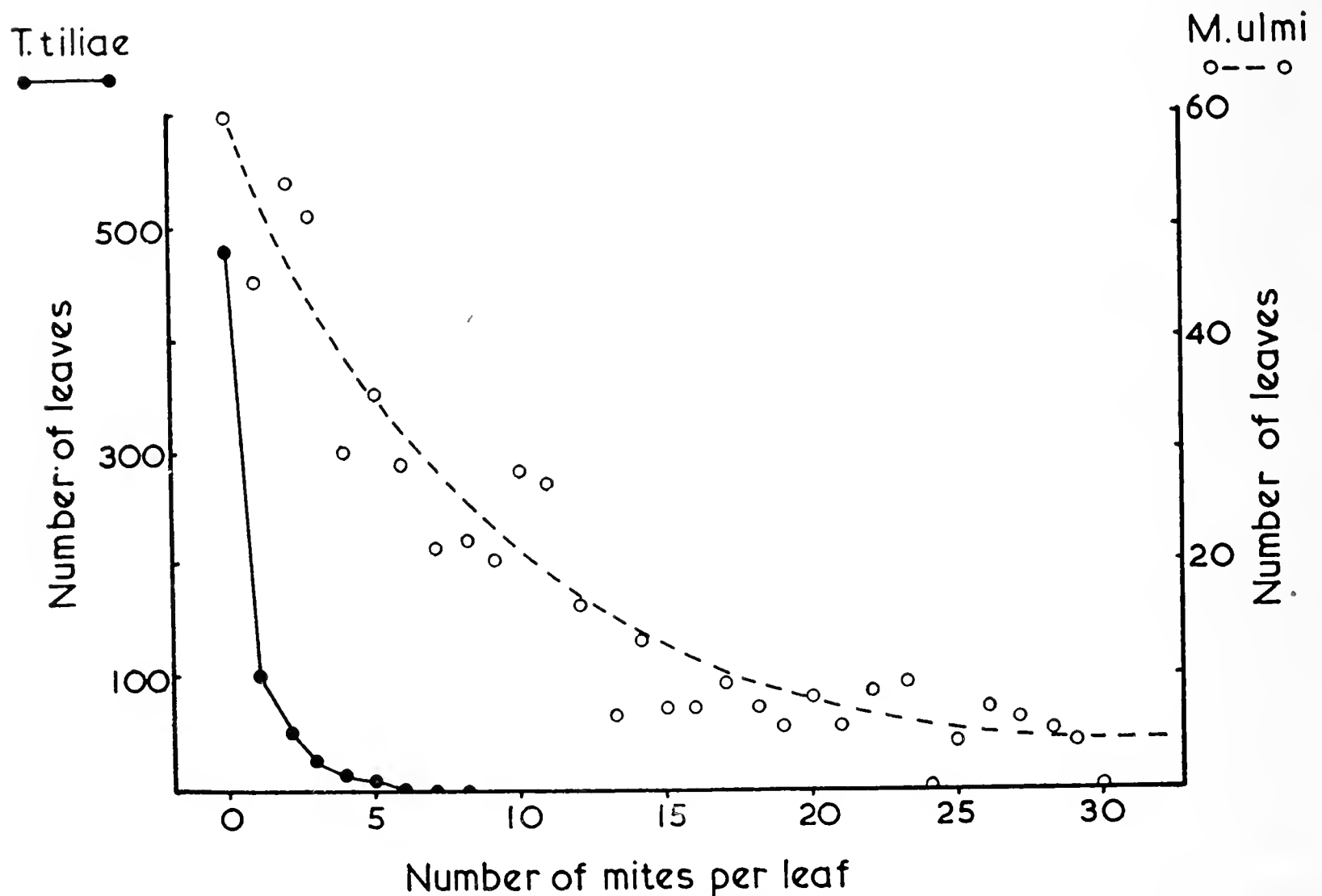


Fig. 3. A comparison of the interleaf distributions of *Typhlodromus tiliae* Oudemans and *Metatetranychus ulmi* (Koch), early summer, 1955.

The distribution of *M. ulmi* during the later parts of the season was not investigated beyond determining that virtually every leaf possessed at least a small population.

#### DISTRIBUTION OF PREDATORS AND PREY ON SHOOTS AND SPURS WITHIN TREES

For this study shoots and spurs were considered as similar ecological units. The distributions of *T. tiliae* and *M. ulmi* were similar on both types of growth in 1954, though the predator was less numerous on shoots; therefore only spurs were considered in 1955. Each leaf was cut from the collected spur and the mites on it recorded immediately. The results from this are shown in Fig. 4; the graph for each period is of one collection taken during that period in 1955. Not all collections showed so clearly-defined distributions, but invariably the trends shown in the graphs were evident and variation in character between samples was slight. There was an average of 10 leaves per spur in early summer, but later, following the shedding of senescent basal leaves in June, only seven leaves were present. Fig. 4 shows that throughout the summer *T. tiliae* was most abundant on younger leaves near the tips of the spurs, though late in the season the population became more diffused.

The picture for *M. ulmi* is somewhat different; in early summer this species occurred most abundantly on the older leaves of the spurs. Basal leaves are the first food encountered by young larvae as they move up twigs from hatching sites in the spring, and they are probably colonized for this reason. As these leaves passed maturity and fell from the trees, *M. ulmi* moved progressively up the spurs until, by mid-summer, it occupied approximately the same position as *T. tiliae*, though somewhat more dis-

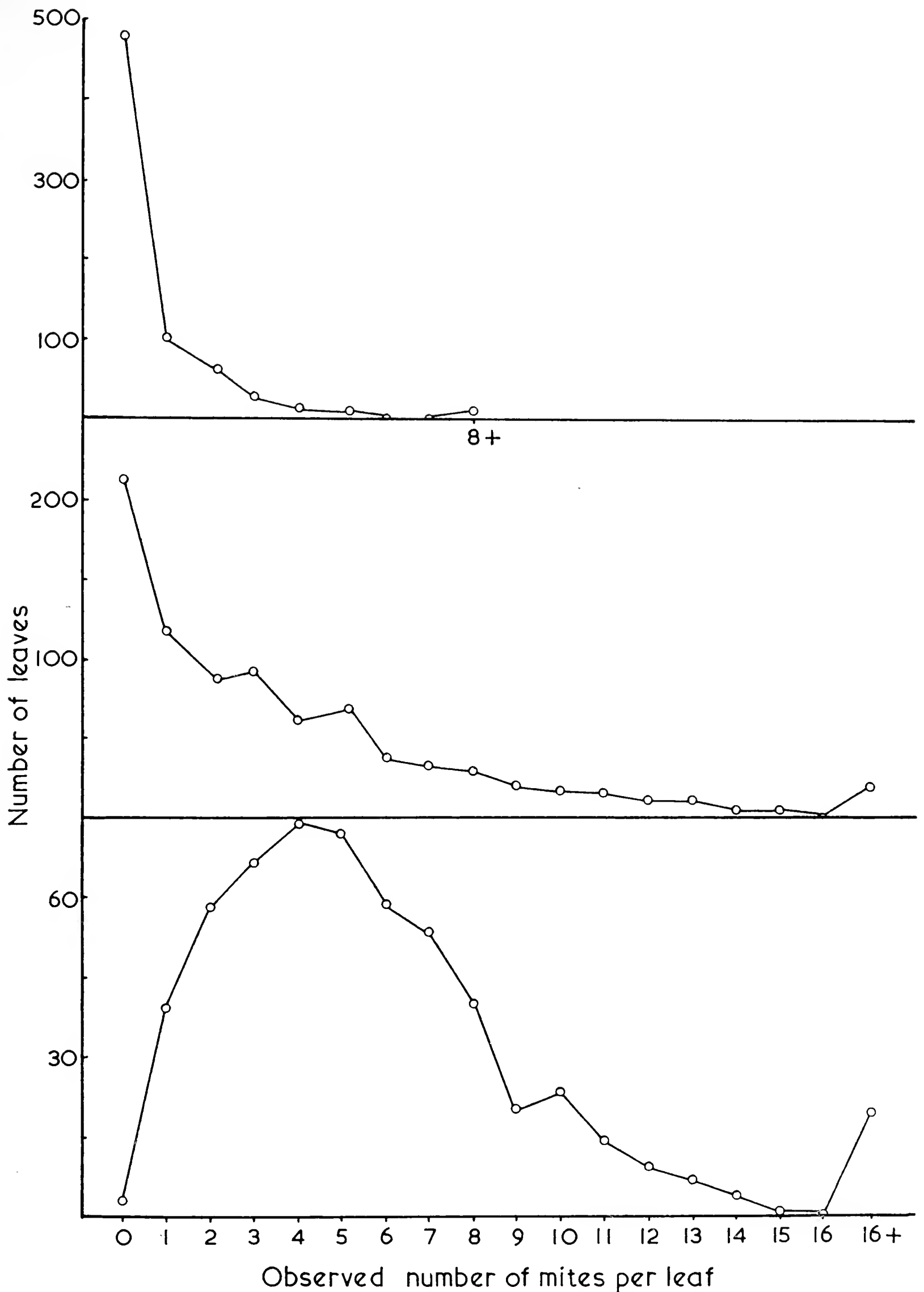


Fig. 4. The distribution of *Typhlodromus tiliae* Oudemans and *Metatetranychus ulmi* (Koch) along fruit spurs of apple throughout the summer. (N.B. leaf 10 is the youngest).

persed. In late summer, *M. ulmi* was distributed uniformly over the spurs, the large leaves generally bearing the largest colonies.

Thus, in early summer, when *M. ulmi* was least abundant and the predator had the best opportunity to effect control, most of the predators would have been located where prey density was least, and most *M. ulmi* would have been on leaves without

*T. tiliae*. Not until mid-summer, when *M. ulmi* had greatly increased in density, would the two populations have intermingled, and in late summer, when *M. ulmi* was uniformly distributed, much of the population again would have been free from predation. This distribution appeared to be stable, and existed at night as well as during the day.

Casual observations suggested that *T. finlandicus* was more uniformly distributed than *T. tiliae* but it was not possible to verify this.

It thus appears that all aspects of the distribution of *T. tiliae* differ from those of *M. ulmi*. On the leaf surface large areas are free from the predators whereas *M. ulmi* has a uniform distribution; variation in distribution between leaves indicates that *T. tiliae* does not colonize all leaves until late summer, whereas *M. ulmi* is found on most leaves from early summer onwards; and *T. tiliae* prefers the youngest leaves on spurs and shoots throughout the summer, whereas *M. ulmi* is most numerous on rosette leaves in spring and early summer, and in late summer has a uniform distribution overlapping that of the predator. Therefore, during much of the season *M. ulmi* is probably able to develop almost free from any controlling influence by *T. tiliae*.

#### THE EFFECTIVENESS OF *T. tiliae* AS A PREDATOR OF *M. ulmi*

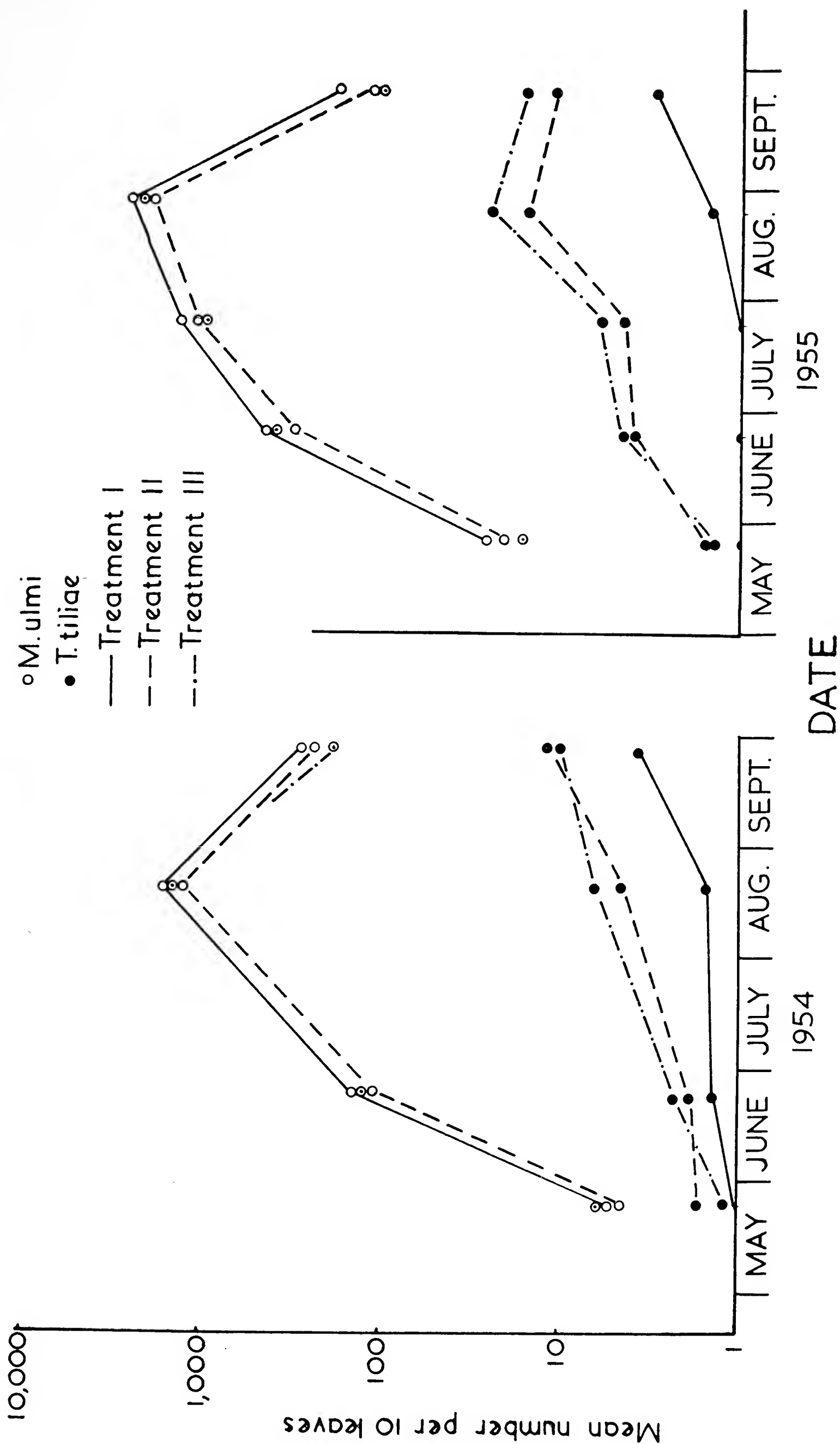
To test the validity of the conclusions on the probable ineffectiveness of *T. tiliae* as a predator of *M. ulmi*, a field experiment was planned that would not depend on chemicals to obtain predator differentials. An orchard of 192 seven-year-old apple trees was available at East Malling during 1954 and 1955. This was divided into 12 16-tree plots and three treatments, as follows, were replicated four times each. Each tree was supported by a stake and the twine between stake and tree fastened to a burlap pad on the trunk. The predacious mites hibernated in this burlap and by removing the pads a tree could be virtually denuded of typhlodromids. Each winter the bands were removed from Treatment I, and untouched on II and III. The bands removed from I were placed on III in an attempt to increase the density of *T. tiliae*. A wash of DNOC/petroleum was applied each winter to all plots, and during the summer one spray of lead arsenate was applied throughout.

During the summer of 1954 four, and in 1955 five, collections of leaves were taken from this orchard. These consisted of 40 leaves per replicate and they were brushed with a Mite Brushing Machine (Henderson and McBurnie, 1943) and the yield of *T. tiliae* and *M. ulmi* recorded. The results of this are shown in Fig. 5. There were four times as many predacious mites in 1954 where the bands were undisturbed as on Treatment I where they were removed. There was no significant difference between the densities of *M. ulmi* on the three treatments, though the two with *T. tiliae* had slightly fewer *M. ulmi* throughout the season. In 1955 the predator was approximately 15 times as numerous on Treatments II and III, where there were densities of 1.6 and 2.7 mites per leaf respectively, as on I, where the maximum density was 0.2 per leaf. Treatment III had a greater population than II, almost certainly as a result of having received the bands removed from I. The numbers of both predator and prey were higher in the second year, probably partly because warm weather stimulated development and partly as a legacy of the high numbers present in the previous autumn. On plots where *T. tiliae* was abundant, the numbers of *M. ulmi* again were not significantly lower than on plots where the predators were scarce.

Damage assessment by an independent observer experienced in this field showed that in each year damage was severe, and that there was no significant difference between treatments. In every case damage far exceeded that tolerated under commercial conditions, and yet on some plots *T. tiliae* was considerably more abundant than under normal orchard conditions.

The effect of this predator was neither masked nor accentuated by the action of insect predators, which showed no differences in density between treatments. In 1955 the macropredators were abundant but, despite this and the mortality caused to *M. ulmi*

Fig. 5. The effect of *Typhlodromus tiliae* Oudemans on *Metatetranychus ulmi* (Koch) in one orchard in 1954 and 1955. The vertical scale is logarithmic and the differences in *M. ulmi* density were not significant at the five per cent level. —>



by the winter wash, damage to the foliage was severe. Thus, over a period of two years *T. tiliae* failed to achieve satisfactory control of *M. ulmi*. Of course, even for this species in southeastern England these results are not conclusive, and possibly over a greater number of years the predator might achieve worthwhile control of the pest. However, additional credence should be given to the results in view of the investigations described earlier.

### CONCLUSIONS

In summation, then, it is the author's belief, and one which seems consistent with the data presented, that phytoseiids, with the possible exception of *T. finlandicus*, are of little actual or potential value in the control of orchard-inhabiting phytophagous mites in southeastern England. This conclusion is largely deductive and based on observations of the character of these mites, but field "proof" has been offered in one instance. It seems evident that typhlodromids are *inefficient* predators and, though it does not necessarily follow that they are *ineffective* predators, field experimentation lends support to this belief.

It is not suggested that this is necessarily true of other phytoseiid species in other parts of the world, as one fact that emerges from the present study is that each species must be treated individually. However, in the absence of precise information concerning their effect, their importance may well have been exaggerated and the present study emphasizes the need for critical investigations to test the validity of the unsupported statements that have sometimes been made.

### ACKNOWLEDGMENTS

This work was conducted at the East Mallong Research Station, England, under the direction of Dr. A. M. Masee, whom the author wishes to thank for his help and encouragement. For the year 1953-1954 the author was in receipt of a Special Scholarship for Overseas Study from the National Research Council of Canada, and this is gratefully acknowledged.

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### DISCUSSION

D. J. KUENEN. Was account taken of the fact that numbers of *Metatetranychus ulmi* and *Typhlodromus* are not independent when counting them for leaf distribution studies?

D. A. CHANT. *Typhlodromus* was counted in derelict orchards with very few *ulmi*, and *Metatetranychus ulmi* in commercial orchards, not treated during the year of investigation and where predators were absent.



# The Role of *Typhlodromus* spp. (Acarina: Phytoseiidae) in British Columbia Apple Orchards<sup>1</sup>

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## ABSTRACT

The family Phytoseiidae is represented by at least 30 species of mites of the genera *Typhlodromus* and *Phytoseius* in southern British Columbia; most of the species are widely distributed but occur in relatively small numbers. *Typhlodromus rhenanus* (Oudemans), *T. occidentalis* Nesbitt, and *Phytoseius macropilis* (Banks), are the common species on fruit trees in the commercial orchard areas.

The distribution of these mites on the leaves indicates that they are not very efficient predators. They are found on the lower leaf surface, primarily along the midrib. In contrast, most of the host mites feed on both surfaces of the leaves and have a more random distribution.

In British Columbia typhlodromids do not produce populations of a similar magnitude to those of phytophagous mites. This is because they have fewer generations, a lower egg production, and a higher winter mortality.

By using the color of ingested food as an indicator of the type of mites consumed it was found that *T. occidentalis* and *T. rhenanus* fed only sparingly on *Metatetranychus ulmi* (Koch) or *Bryobia* spp. These predators fed chiefly on free-living eriophyid mites, but were not observed to control infestations in commercial orchards. However, they may be of some commercial value in limiting the numbers of *Tetranychus telarius* (L.) and *Eotetranychus carpini borealis* (Ewing).

## INTRODUCTION

The role of *Typhlodromus* spp. as possible biological control agents of phytophagous mites was first indicated by Parrott *et al.* (1906) who considered that a gamasid mite, *Seius* (= *T.*) *pomi* Parrott, materially assisted in reducing the numbers of the pear leaf blister mite, *Eriophyes pyri* (Pgst.). The general biology of that typhlodromid was first studied in Canada by Gilliatt (1935) who reported that typhlodromid mites were probably the most important predators on the European red mite, *Metatetranychus ulmi* (Koch), in Nova Scotia. Interest in these predators became world wide following publication of the taxonomic works of Garman (1948) and Nesbitt (1951). Because of the promising results obtained with phytoseiid mites in other fruit growing areas, (Collyer, 1949; Lord, 1949; Smith and Summers, 1949; Clancy and Pollard, 1952; Herbert, 1952), a co-operative project was begun in 1951 by the Biological Control and the Fruit Insects Units, Science Service, Canada Department of Agriculture, to determine the value of these predators in the natural control of orchard mites in British Columbia.

The chemical control of phytophagous mites is a major problem in British Columbia apple orchards. More than seven species occur here: many differ markedly from one another in life-histories and habits; consequently, different chemical control programs are necessary. These seven species are: the European red mite, *M. ulmi*, the brown mite, *Byrobia arborea* Morgan and Anderson, the two-spotted spider mite, *Tetranychus telarius* (L.), the yellow spider mite, *Eotetranychus carpini borealis* (Ewing), the Mcdaniel spider mite, *Tetranychus mcdanieli* McGregor, the pear leaf blister mite, *E. pyri*, and the apple rust mite *Vasates schlechtendali* (Nal.). Of these species *M. ulmi* has caused the most damage. Its control has been an annual problem in most areas for over 15 years; but in some years its importance has been superseded, or complemented, by other mites. *E. pyri*, *V. schlechtendali*, and *B. arborea* are the prevalent species in nonsprayed, neglected orchards. Only the first two of these species cause extensive damage.

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Thirty species of phytoseiid mites (genera *Typhlodromus* Scheuten and *Phytoseius* Ribaga) occur on native and cultivated plants in southern British Columbia. Fifteen of these were found by the authors on apple and other fruit trees. The species are: *T. (T.) bakeri* (Garman), *T. (T.) conspicuus* (Garman), *T. (T.)* new species (see Cunliffe & Baker, 1953), *T. (T.) occidentalis* Nesbitt, *T. (T.) arboreus* Chant, *T. (T.) rhenanus* (Oudemans), *T. (T.) soleiger* (Ribaga), *T. (T.) tiliae* (Oudemans), *T. (A.) andersoni* Chant, *T. (A.) fallacis* (Garman), *T. (A.) finlandicus* (Oudemans), *T. (A.) okanaganensis* Chant, and *P. macropilis* (Banks) (= *spoofti* (Oudemans)). The recorded geographical distributions and the plants from which the 30 species have been collected will be published elsewhere (Anderson et al., in press).

Only three of the 15 species found on fruit trees are sufficiently abundant in the commercial fruit growing areas to warrant attention as possible biological control agents of phytophagous mites: *T. occidentalis* and *T. rhenanus* in the Okanagan Valley, and *P. macropilis* and *T. rhenanus* in the Kootenay Valley.

## METHODS

The ecological studies were conducted in the semi-arid Okanagan Valley, and were supplemented by field observations and collections in other areas of British Columbia. Climatic conditions differ widely between these areas, and consequently, the complex of species differ markedly throughout the province. Most of the work was done in nonsprayed plots in commercial orchards or in neglected orchards. Detailed information was obtained from samples of ten leaves per tree taken weekly or twice weekly from five trees per plot during the growing season. The mites were removed from the leaves by a mite brushing machine (Henderson and McBurnie, 1943) and counted under a stereoscopic microscope. Field studies were supplemented by laboratory observations on typhlodromids reared in modified Huffaker cells with various species of phytophagous mites (Ballard, 1954).

## RESULTS

### RELATIVE DISTRIBUTION OF TYPHLODROMUS SPP. AND PHYTOPHAGOUS MITES ON THE FOLIAGE

This discussion is restricted to the distribution of the predominant species, *T. rhenanus* and *T. occidentalis*, on individual leaves, as these species are rarely found on the bark of twigs or fruit spurs during the growing season but are confined to the lower surfaces of the leaves. On apple leaves that have comparatively little pubescence they deposit their eggs mainly along the mid-rib or in the axis of the mid-rib and lateral veins. The latter oviposition site is also characteristic on cherry leaves that are practically devoid of pubescence. On varieties of apple that possess heavy pubescence, a few eggs are laid also along the lateral veins and sometimes in the inter-veinal areas. The active stages have a somewhat similar distribution.

This restricted distribution indicates that these typhlodromids are not efficient predators because the pattern is not correlated with most of the phytophagous mites on which they feed. In warm weather, for example, one half of both the eggs and active stages of *M. ulmi* are on the upper surface of the leaf, and consequently, are out of range of predation by their typhlodromid enemies. Of all the important phytophagous species of orchard mites in this area only *T. telarius* and *E. carpini borealis* have a similar distribution to typhlodromids. However, this similarity exists only during the early stages of the infestation; as these phytophagous mites become numerous they too disperse over the undersurface of the leaf.

### RELATIVE POPULATIONS OF TYPHLODROMUS SPP. AND METATETRANYCHUS ULMI

In nonsprayed, neglected orchards the numbers of typhlodromid mites are relatively constant from year to year. In two such orchards sampled at monthly intervals for five consecutive years the seasonal average population varied from 0.33 to 1.75 mites per leaf in one orchard and from 0.29 to 0.43 per leaf in the second orchard.

By contrast, in a nonsprayed commercial block sampled during the same period the seasonal average varied from 0.06 to 5.45 per leaf. The maximum numbers occurred two years after spraying was discontinued and the minimum four years after.

The studies of MacGill (1939), Smith and Summers (1949), and Ballard (1954), indicate that under laboratory conditions of high temperature certain species of typhlodromids have a high reproductive potential. Ballard found that at a constant temperature of 78°F., *T. fallacis* completed a generation within less than a week and that each female laid over 40 eggs. Smith and Summers concluded from their laboratory studies that "*Hypoaspis*" (= *Phytoseiulus*) *macropilis* (Banks) could build up populations more rapidly than could its host, *Tetranychus bimaculatus* Harvey (= *telarius* L.). However, Chant (in preparation) reported that in insectary rearings, at temperatures practically comparable to field conditions, *T. tiliae* completed a generation in about three weeks and had a maximum of four generations per season. This number of generations together with an average egg production of only one egg every three to four days would result in a much lower reproductive potential than that of most phytophagous mites. Field sampling in British Columbia corroborates Chant's work. In 1952, for example, the overwintering typhlodromids in a nonsprayed commercial apple block began to lay eggs about the third week of May, approximately two weeks after *M. ulmi* had begun to lay the first summer eggs. The first summer generations of typhlodromids and *M. ulmi* were completed one month later. Thus, while typhlodromids produced one generation up to the end of June, *M. ulmi* had developed a spring generation (from winter eggs) plus a summer generation. During this spring development the numbers of *Typhlodromus* spp. increased from 0.5 to 0.7 per leaf while those of *M. ulmi* increased from 0.1 to 6.5 per leaf. Obviously the typhlodromid population was developing at a slower rate than that of *M. ulmi*. The greatest increase we observed in the numbers of typhlodromids throughout the growing season was from 0.5 to 11 per leaf—a 22-fold increase; *M. ulmi*, on the other hand increased more than three times as much. When populations of *Typhlodromus* spp. reach their peak, usually in late August or September, the ratio of active stages to eggs has approximated 3.8 to 1. Under the same environmental conditions *M. ulmi* reached its greatest numbers in July, when the ratio of active stages to eggs averaged about 1 to 3.6. Allowing for the shorter incubation period of typhlodromid eggs, the data still indicate that more eggs are laid by each female of *M. ulmi* than by that of *Typhlodromus* spp.

In Fig. 2 populations of *M. ulmi* and typhlodromids are compared in a nonsprayed block of a commercial orchard. During the first year, when no sprays were applied, typhlodromids did not enter the trees until late July, when the numbers of *M. ulmi* averaged 35.5 per leaf. Six weeks later, and coincident with a sharp decline in the numbers of *M. ulmi*, typhlodromids reached their peak of 1.06 per leaf. This suggested that the predator might be responsible for the reduction in numbers of the phytophagous mite. The following year the numbers of *M. ulmi* and of typhlodromids were closely followed by sampling twice a week from May to October. *M. ulmi* populations increased steadily up to the latter part of July, when they averaged 126.4 per leaf. As in 1951, a sharp decrease occurred during August. In this period the numbers of typhlodromids increased to 5.7 per leaf and the increase continued throughout the fall. By the end of September there were almost 11 typhlodromids per leaf, the greatest number so far observed on apple trees in the Okanagan Valley. If typhlodromids were important predators, it might be expected that a balance would occur between the predator and *M. ulmi* the following year. However, this did not occur; *M. ulmi* populations reached an average of 118.3 per leaf in August, while typhlodromids did not exceed 0.25 per leaf at any time during the year.

Newcomer and Yothers (1929), concluded that natural enemies were responsible for the sudden annual decline of *M. ulmi* each August. Their conclusions have no doubt influenced other workers who observed similar negative correlations between *M. ulmi* and typhlodromids at that time of year. The decline of *M. ulmi* after July, however, appears to be an annual occurrence in sprayed orchards in British Columbia but it has not been established if this phenomenon is inherent in the biology of the mite or if it is due to insect predators. It is evident, however, that predation by typhlodromid mites is not the cause of the August decline. In support of that opinion and as indicated

in Fig. 1, a decline corresponding to that on the nonsprayed check plot occurred on DDT-sprayed trees where no typhlodromids were present. Gilliatt (1935), reported that typhlodromids are effective predators in Nova Scotia because they are actively predacious from early spring until late fall when all winter eggs of *M. ulmi* have been deposited. It might have been expected, therefore, that large populations of typhlodromids, such as occurred in the autumn of 1952, would have materially reduced the

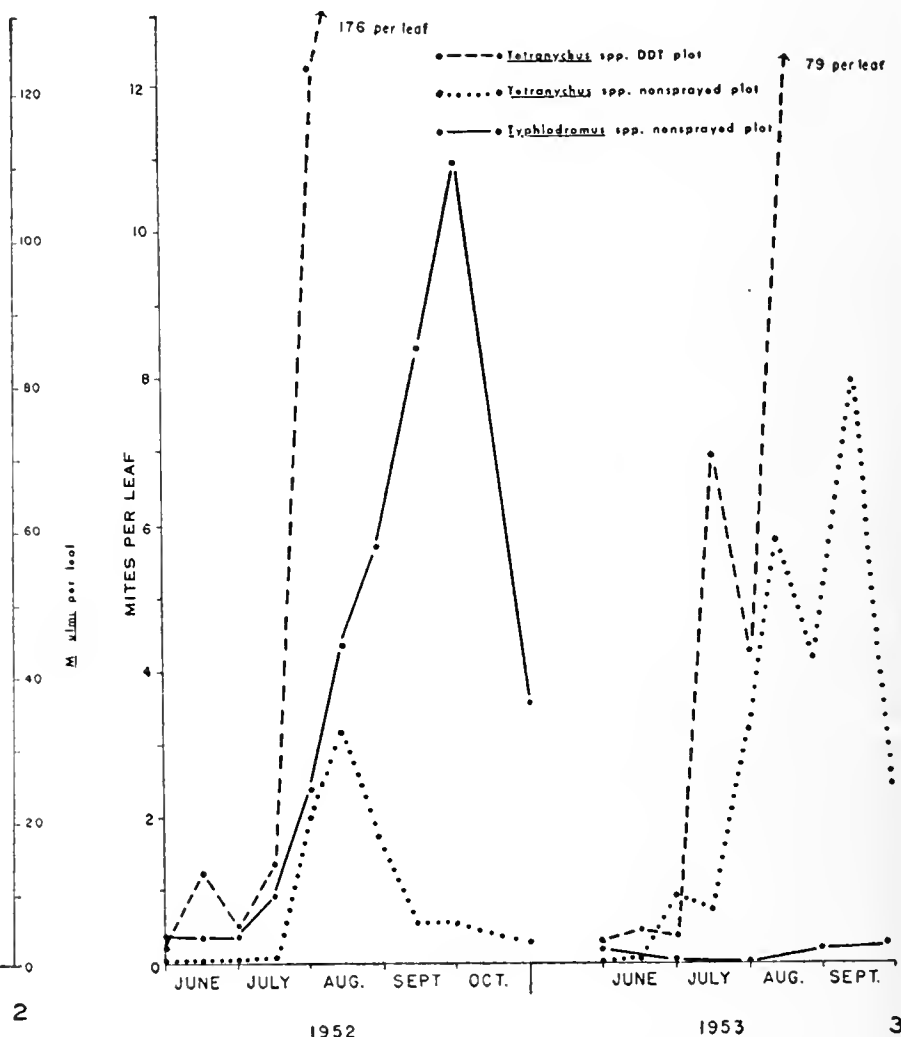
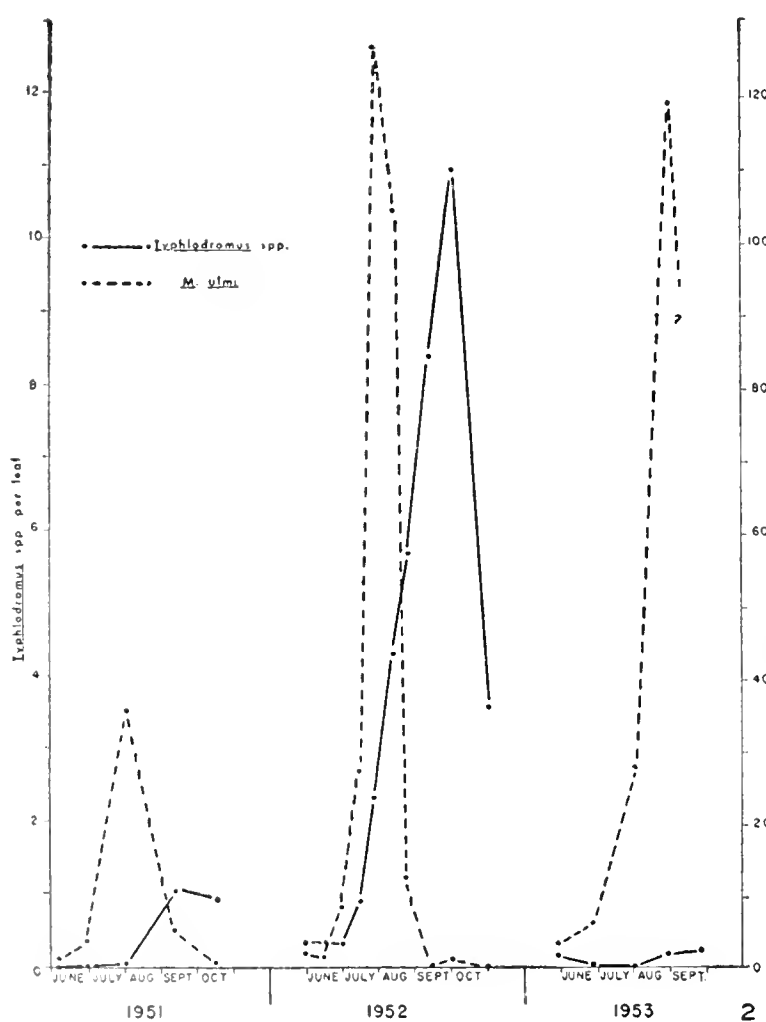
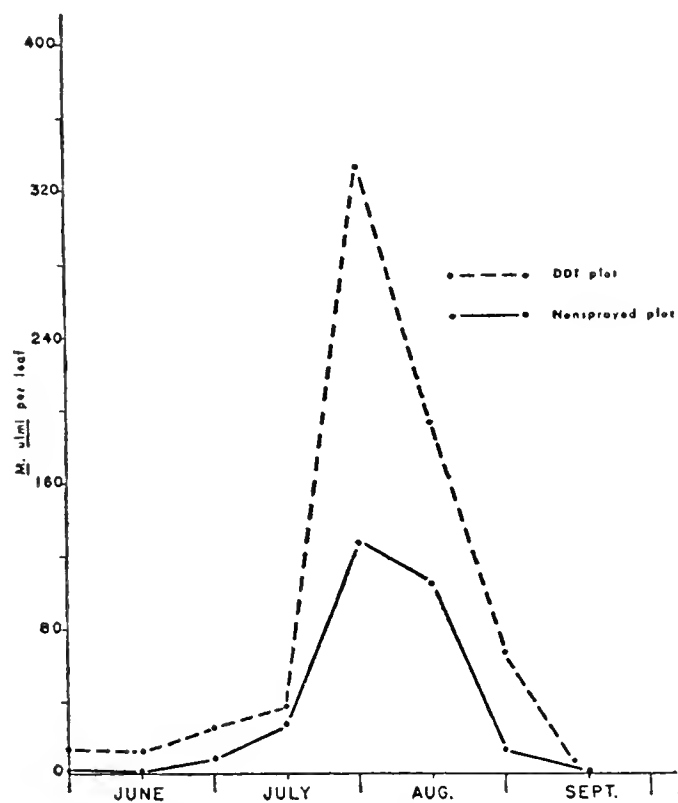


Fig. 1. Numbers per leaf of *Metatetranychus ulmi* (Koch) on Yellow Transparent apple trees at Summerland, B.C., in 1952, showing "August decline" in a DDT-sprayed plot with no typhlodromids and in a nonsprayed plot with many typhlodromids.

Fig. 2. Numbers per leaf of *Typhlodromus* spp. and *Metatetranychus ulmi* (Koch) on nonsprayed Yellow Transparent apple trees at Summerland, B.C., in three years.

Fig. 3. Numbers per leaf of tetranychids (*Tetranychus telarius* (L.) and *Eotetranychus carpini borealis* (Ewing)), and of *Typhlodromus* spp. on Yellow Transparent trees at Summerland, B.C., on DDT-sprayed and nonsprayed plots in two years. Note the apparent negative correlation between the numbers of phytophagous and of predacious mites.



numbers of overwintering eggs of *M. ulmi* and hence, the size of the following spring population. That, however, did not occur; spring populations of *M. ulmi* were approximately equal from 1951 to 1953, though the number of typhlodromids present in the fall ranged from one per leaf in 1951 to 10 per leaf in 1952.

Winter mortality appears to be one of the most important of the various factors which limit population levels of typhlodromids. In the British Columbia studies though typhlodromids sometimes were relatively numerous in late summer, invariably they were scarce the following spring. In two locations where collections were taken in October, 1952 and October, 1953, the numbers per ten leaves averaged 93 and 14 respectively. By spring these numbers had become 3 and 0.5 respectively, as shown by collections taken in May in each of the following years. Even in England, where minimum winter temperatures are not as low as in the Okanagan Valley, winter mortality of *T. tiliae* may reach 97 per cent (Chant, in preparation).

#### PREDATION ON OTHER PHYTOPHAGOUS MITES

Though observations suggest that *T. occidentalis* and *T. rhenanus* feed chiefly on eriophyid mites in British Columbia apple orchards, there is little evidence that they are capable of reducing heavy infestations of these mites to a commercial level. In neglected, nonsprayed orchards *V. schlechtendali* often causes extensive bronzing of the foliage. Samples taken on a number of occasions from such orchards have shown, that, though free-living eriophyids were the only phytophagous mites present, and the numbers of typhlodromids were relatively high (one to two per leaf), the predators were not effectively reducing the eriophyids. Similar observations have been made in commercial cherry, prune, peach, and apple orchards.

Parrott *et al.* (1906), reported that *S. pomi* was an important control agent of the pear leaf blister mite, *E. pyri*, in New York. Their findings, however, have never been verified by other workers. It seems unlikely that typhlodromids could exert a measurable effect in controlling *E. pyri* because it spends most of the summer in a spongy cellular blister which cannot be penetrated by the predator. *E. pyri* can, however, be preyed upon when it migrates to form new blisters and when it leaves the blister in the autumn to hibernate beneath the bud scales. As mentioned previously, this mite causes extensive damage in nonsprayed orchards in this area.

Typhlodromids may be important predators of the two web spinning mites, *T. telarius* and *E. carpini borealis*. Both of these mites have a similar distribution on the leaves to that of the predator; and the life-history of the typhlodromids is more closely synchronized with these mites than with *M. ulmi* or *B. arborea*. Members of the former group are generally not very common in the early part of the season; they become prevalent during mid-summer and usually reach peak populations in late August or early September. As indicated in Fig. 2, *Typhlodromus* spp. are found in their greatest numbers about the same time. *T. telarius* often develops in large numbers on the cover crops and weeds in the early summer and subsequently migrates into the trees. On herbaceous plants it is subject to attack by *Typhlodromus cucumeris* Oudemans, an active predator occurring only on low-growing herbaceous plants. The importance of *T. cucumeris* as a biological control agent has not been established in this respect, but field observations and laboratory studies have shown it to be one of the more voracious of the typhlodromids.

The role of *Typhlodromus* spp. in the control of *T. telarius* and *E. carpini borealis* is difficult to assess as these pests are usually found in association with other tetranychids and eriophyids. However, in a nonsprayed block of a commercial orchard where these two species co-existed there appeared to be a negative correlation between these phytophagous mites and the number of typhlodromids as compared with a DDT-sprayed block (Fig. 3). These results are based on a single experiment; it would be premature to attribute the entire reduction of the tetranychids to typhlodromid predation, particularly as the role of insect predators was unknown.

#### COLOR AS AN INDEX OF FEEDING

The integument of typhlodromids, unlike that of many predators, is semi-transparent and the color of ingested food, as seen through the body wall is distinctive.



Coloration is an aid in determining food preferences and, to a limited extent, the amount of feeding.

The three most prominent colors of typhlodromids are red, greenish-black, and yellowish-brown. The shade and degree of coloration varies considerably, depending on the variation in color of the phytophagous mites and the period elapsed after the last feed. Reddish-brown, red, and pink typhlodromids result from feeding on all stages of *M. ulmi* or on the eggs and larvae of *Bryobia* spp. However, both of these phytophagous mites vary in color from green to reddish-brown and these colors are imparted to the predator. Specimens of *T. cucumeris* that are engorged with the body fluids of *B. praetiosa* Koch may even be a dark greenish-black color. As a result of having fed on the tetranychids, *T. telarius* or *E. carpini borealis*, or on eriophyid mites the color of the typhlodromid may vary from light yellow to yellowish-brown. Unless observations are made on pure cultures of each of the three phytophagous mites, it is difficult to determine the species preyed upon.

The color of ingested mites may remain in the body of the typhlodromid for several days but it fades considerably during this period. Chant (in preparation) showed that the red color of *T. tiliae* engorged on *M. ulmi* gradually fades to brown and all color disappears within five days or less. Eighty per cent of the females of *T. tiliae* had colored intestines three days after feeding; four days after only 25 per cent were colored. The use of typhlodromid coloration as an index of the type of food consumed must be used with caution in the field as it is complicated not only by the fading of colors but also by the phytophagous and cannibalistic habits of these predators.

Since Gilliatt (1935) studied *S. pomi* in Nova Scotia surprisingly few workers have mentioned the value of color for indicating the nature of the food. Gilliatt found that, in general, most adults were pale in color and without characteristic markings; occasional individuals however, had brown, red or wine colored markings, and these he thought had fed on *M. ulmi*. Gilliatt's remarks concerning intestinal coloration give little support to his belief that *S. pomi* was one of the most important predators of *M. ulmi*.

In British Columbia over 5,000 typhlodromids (*T. rhenanus* and *T. occidentalis*) were examined for color during August and September, 1952. They were collected in a commercial orchard infested with *V. schlectandali*, *T. telarius*, *E. carpini borealis*, and *M. ulmi*. Of these typhlodromids, 70.1 per cent were colorless indicating the majority had not fed on phytophagous mites for at least three days. Only 0.2 per cent carried the red coloration that indicates recent feeding on *M. ulmi*. The remaining 29.7 per cent were various shades of brown. The small percentage of red specimens suggests that the brown coloration was induced by feeding on *V. schlectandali*, *E. carpini borealis*, or *T. telarius* and did not result from the fading of ingested red matter. The largest percentage of red typhlodromids noted in the course of this work occurred in a commercial prune orchard that contained a pure population of *T. occidentalis* associated with a heavy infestation of *M. ulmi* and moderate numbers of *V. schlectandali* and *T. telarius*. Here 57.4 per cent of the *T. occidentalis* were colorless, 25.5 per cent were red, and 17.1 per cent were yellowish-brown. Assuming that color can be used as a reliable criterion of feeding habits, the evidence presented here shows conclusively that *T. occidentalis* and *T. rhenanus* are not important predators of *M. ulmi* in the Okanagan Valley of British Columbia. *T. tiliae*, which is common on the Pacific Coast, might be expected to effect measurable control of *M. ulmi* and *Bryobia* spp. in that area, because there, both the actual number and the percentage of red specimens are high. Nevertheless, Chant (in preparation) showed that in England, where approximately half the population of *T. tiliae* is colored, this predator is not an effective control agent of *M. ulmi*.

Most of the typhlodromids collected from native and cultivated plants in various parts of the province are colorless. As a large proportion of them were collected on plants free from phytophagous mites, there is fair evidence that the typhlodromids are phytophagous; certainly they are not obligate predators. Where typhlodromids were found in association with free living eriophids only, a greater portion of the population was colored than where they occurred with *M. ulmi*. For example, in a prune orchard

infested principally with eriophyids, where the average number of *T. occidentalis* was three per leaf, 45.5 per cent of the predators were brown. Similar numbers of colored typhlodromids have been observed in association with eriophyids in commercial peach and cherry orchards. In most cases however, there was no suggestion of effective biological control.

### ACKNOWLEDGMENTS

Dr. D. A. Chant, Entomology Laboratory, Belleville, Ont., took part in these studies in 1951 and 1952. The authors wish to acknowledge his help both then and later, when he assisted in identifying predacious mites.

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# Natural Control of Phytophagous Mites (Tetranychidae and Eriophyidae) in Ontario Peach Orchards<sup>1</sup>

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## ABSTRACT

Among at least 28 species of predators attacking the European red mite, *Metatetranychus ulmi* (Koch), in Ontario peach orchards, *Typhlodromus rhenanus* Oudms., *Stethorus punctillum* Weise, and *Haplothrips faurei* Hood are the most important; *Chrysopa plorabunda* Fitch and *C. rufilabris* Burm. may occasionally have some effect. Most species are relatively scarce in the spring and seldom reach effective numbers until some time in August and September after the natural decline of the European red mite. *S. punctillum* and *H. faurei* have been greatly reduced even in unsprayed orchards since DDT and parathion came into use in the district. Nevertheless, populations of the European red mite have remained very low in some orchards not receiving insecticides, where other predators are also scarce; this questions the importance of predators as natural control agencies but results are not yet conclusive.

Most of the predacious species also attack the two-spotted spider mite, *Tetranychus telarius* (L.), which is especially susceptible to predation owing to its colonial habit, although weather factors are probably equally important control agencies. Predators of the clover mite, *Bryobia praetiosa* Koch, are fewer. *T. rhenanus* and other phytoseiid mites are the only common predators of the peach silver mite, *Vasates cornutus* (Banks).

## INTRODUCTION

From 1931 to 1935 the influence of predators on the oriental fruit moth, *Grapholitha molesta* (Busck), was investigated in a number of peach orchards in the Niagara Peninsula, Ontario. Much information on the prevalence and habits of predators attacking phytophagous mites was incidentally obtained at the same time. Since 1946 much more information on the predators has been accumulated during work on the effects of pesticides on biological balance in peach orchards.

This paper is a summary of the occurrence and habits of the more effective predators encountered during the investigations mentioned. Work on phytoseiid mites, and on the influence of predators in general, is still under way, and a final evaluation cannot be attempted at this time.

## METHODS OF STUDY

During 1931 to 1935, one-hour counts of macroscopic forms on the leaves were made weekly on both young and mature peach trees in four orchards distributed between Niagara-on-the-Lake and Grimsby. These orchards received a dormant spray, usually of lime sulphur, and usually two summer sprays of wettable sulphur, the first about the beginning of June when few leaves had expanded and the second shortly before harvest. On the predominant variety Elberta the last spray was usually applied in late August, so that the foliage was free of pesticides throughout most of the summer.

All the leaves on about one foot of twig were examined on each tree encountered as the observer followed an irregular course through the orchard. Some sample counts showed that about 1,000 leaves were examined per hour. This method allowed direct observation of the habits of the predators and showed their relative abundance, but it did not correlate their numbers with those of their mite prey except in a general way. They were very important in revealing the prevalence of both predators and prey at a time before such drastic insecticides as DDT and parathion were used.

The studies begun in 1946 have been carried on in two to five orchards annually. Most of these were commercial orchards divided into plots of approximately  $\frac{1}{2}$  to 1 acre, which received various spray treatments. Most observations on predators were conducted in plots that received sulphur sprays only. Since 1952 plots that did not receive any sprays have also been used. Direct observation of foliage in the orchards

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was continued to some extent but most effort was concentrated on sampling the populations of both predators and prey by means of leaf samples examined under a binocular microscope in the laboratory and by jarring or brushing branches in the orchard. These procedures and their limitations have been described elsewhere (Putman, 1955). The very low numbers of many predacious species made it impracticable to determine their populations very precisely, but at least the upper limits of their numbers were determined with reasonable accuracy.

### PHYTOPHAGOUS MITES ON PEACH

#### EUROPEAN RED MITE, *Metatetranychus ulmi* (Koch)

During the earlier studies, from 1931 to 1935, the European red mite was comparatively scarce, the maximum numbers in most orchards and in most seasons probably not exceeding one mite per leaf. Subsequently the mite showed sporadic increases, although injurious infestations were very infrequent before the general use of DDT in commercial orchards in 1947. In most orchards injury is now prevented only by routine use of acaricides.

High populations of the European red mite on peach follow a characteristic seasonal trend, similar to that reported by many authors on other hosts, that influences the effectiveness of predators but is independent of their activity. The larvae hatch from the overwintered eggs as the leaves are unfolding and settle on the small, lower leaves of the shoots, where most remain until they become adults. These concentrations are very vulnerable to predation. The first-generation adults disperse widely, and as the foliage area is increasing very rapidly the numbers of mites per unit area, and their vulnerability, decrease. As twig growth slows in late June the mites increase very rapidly and reach maximum numbers about the end of July or in early August, or rarely later in August, and then suddenly drop to a much lower level. Dense populations are thus present for too short a time to allow much multiplication of those predators that require a high density of prey for development. Moderate populations of the mite, even below the economic level, may follow a similar seasonal trend with lower fluctuations, but populations that are initially very low in the spring may show a gradual increase until September.

#### TWO-SPOTTED SPIDER MITE, *Tetranychus telarius* (L.)

Injurious infestations of the two-spotted spider mite occurred in peach orchards only after prolonged treatment with DDT, and even there they were erratic and much less serious than those of the European red mite. The seasonal trend of this species is very different from that of the European red mite as populations typically build up more slowly and continue to increase until some time in September or early October. Its colonial habit renders the two-spotted spider mite more susceptible to predation than the European red mite.

#### CLOVER MITE, *Bryobia praetiosa* Koch

The clover mite was conspicuous only in plots that did not receive any sulphur sprays. As yet it is of no economic importance.

#### PEACH SILVER MITE, *Vasates cornutus* (Banks)

The peach silver mite was generally scarce in sulphur-sprayed orchards. Where sulphur was not used it was erratic but no very high populations were seen in the observation orchards.

### PREDATORS

Among at least 28 species of predators found to attack phytophagous mites in local peach orchards, the only ones common enough to have any appreciable influence on the mites are the phytoseiid mite *Typhlodromus rhenanus* Oudms., the thrips *Haplothrips faurei* Hood, the coccinellid *Stethorus punctillum* Weise, and possibly the chrysopids *Chrysopa plorabunda* Fitch and *C. rufilabris* Burm.

#### *Typhlodromus rhenanus* Oudms.

*T. rhenanus* is the most abundant and generally distributed of the 8 species of phytoseiids found on peach trees to date. In the orchards it was observed feeding on the active stages of the European red mite, larvae of the clover mite, and on the peach silver mite. In the laboratory it bred freely on the active stages of the European red



mite. The young stages could not penetrate the summer eggs of this mite; older nymphs occasionally did so but they could not reach maturity on eggs alone. Some adults of *T. rhenanus* also punctured the summer eggs but they were unsuccessful in most of the many attempts observed and they soon died when confined with the eggs alone. Winter eggs were not attacked at all.

Both eggs and active stages of the two-spotted spider mite were readily eaten by *T. rhenanus* in the laboratory.

Eggs of the clover mite were not attacked. Immature clover mites, especially the larvae, were eaten by both adult and immature stages of the *T. rhenanus* predators but adult clover mites apparently could not be captured unless they were disabled.

*T. rhenanus* fed readily on the peach silver mite in the field and laboratory, but no attempt was made to rear the immature stages of the predator on this prey. Circumstantial evidence suggested that this species is often an important and sometimes the chief prey of *T. rhenanus*.

The sampling of phytoseiine populations has presented some difficulties not fully solved. Numbers on the leaves are only about half as large as those on the twigs, where many of the mites rest in the axils of buds, under old bud scales, and other sheltered places. They move freely between leaves and twigs and so form a single effective population.

Even in plots that had not received any pesticides for a number of years the spring population of *T. rhenanus* was very small. Frequently none were found in 500-leaf samples during June, although search of the twigs usually revealed a few. They usually showed marked increase in late July, and reached a maximum during the latter half of September. They then decreased rapidly but a few persisted on the foliage to late October after the beginning of leaf-fall. Population counts made in an unsprayed plot in 1952 are representative of the seasonal trend: the numbers of phytoseiids, mostly *T. rhenanus*, calculated per 100 leaves on June 2, on six counts at two-week intervals from June 26 to September 9, and on October 7 and 22 were 0, 1, 1, 8, 14, 36, 57, 6, and 2. The maximum of 57 was reached on September 9; in plots more frequently sampled the maximum was usually reached later in the month.

The value of 57 phytoseiids per 100 leaves given above is the absolute maximum found in any peach plot to date. Allowing for those present on the twigs, the actual effective population would lie between 150 and 200 per 100 leaves. Such numbers have seldom been approached in most plots, even in non-sprayed ones with abundant prey, and in some orchards they are negligible.

The small spring populations and slow build-up of *T. rhenanus* in peach orchards limit their effectiveness against early season infestations of the European red mite unless these are very low. After the usual crash of the European red mite population, however, the numbers of these predators may approach or even exceed those of the prey during late August and September, so that *T. rhenanus* is potentially highly effective in reducing the part of the prey population that produces the winter eggs. Alternative prey, the clover mite and the peach silver mite, also reach maximum numbers about the same time. The relative attractiveness of the three prey species is not known, but the presence of large numbers of the peach silver mite sometimes found on the foliage and smaller numbers of the clover mite on the twigs could conceivably reduce the extent of predation upon the European red mite. Much further investigation on populations, relative attractiveness of different prey, and numbers of prey consumed per individual predator is needed to elucidate the role of phytoseiids in the natural control of the European red mite.

#### *Haplothrips faurei* Hood

An account of the biology and occurrence in peach orchards of predacious thrips identified as *Haplothrips subtilissimus* Hal. was published by Putman (1942). In 1952 some specimens reared during that investigation were submitted to Miss Kellie O'Neill, United States Department of Agriculture, Washington, D.C., who stated (*in litt.*) they belonged to the species known in America as *H. faurei* Hood. She also said that this species was possibly synonymous with the European *subtilissimus*.

*H. faurei* is a general predator in both larval and adult stages on the eggs and other relatively inactive forms of mites and insects (Putman, 1942; McPhee, 1953), and is one of the more effective predators of the European red mite.

In 1947 adults emerged from ground litter on a wooded bank adjacent to an orchard as early as April 23, and they were collected from peach trees by April 29 in 1948. The comparatively small spring population of this species found in peach orchards, even where it was common the previous fall, indicated a high winter mortality, possibly because it cannot find suitable hibernation sites in cleanly cultivated orchards. It was not recovered during careful examination of the bark in a number of orchards during winter, and its high humidity requirements should preclude hibernation above the soil litter.

Despite its apparently weak flight *H. faurei* disperses readily and before DDT was used it usually appeared soon after an incipient outbreak of the European red mite. Its rate of increase in peach orchards was much lower than the high potential rate revealed experimentally (Putman, 1942). High humidity requirements may be a limiting factor in local orchards with their high summer temperatures and frequent droughts. The freedom of peach leaves from pubescence which would afford shelter for the inactive prepupal and pupal stages and place of attachment for the eggs may also make a peach tree a less favourable habitat.

The numbers of *H. faurei* usually reached a seasonal peak in late August and early September; larvae were collected as late as October 7, and adults till November 16, when they were feeding on winter eggs of the European red mite. Destruction of these eggs was at times extensive, although its exact extent could not be determined owing to concurrent predation by other species.

During 1931 to 1935 *H. faurei* was relatively uncommon in local orchards, primarily because of the scarcity of suitable prey, although the relatively light program of sulphur sprays may have helped to reduce the population. Lord (1949) and MacPhee (1953) showed that sulphur was detrimental to this species. Paradoxically, *H. faurei* became much more abundant immediately after DDT was added to the peach spray program. In 1947 DDT was applied only in a few orchards and on later maturing varieties; these usually developed heavy infestations of the European red mite, which persisted the following season unless effective acaricides were used. *H. faurei* became common in many of these infestations in 1948; in one experimental plot the population reached 14 per 100 leaves in July. Spraying of practically all orchards with DDT later that season reduced it to a very low level where it has remained ever since. Even completely unsprayed plots in moderate sized orchards with abundant prey now contain very few, a population of one per 1,000 leaves being exceptional. Outside of the intensive orchard districts it remained common, for Mr. J. H. H. Phillips of this laboratory reports cases of almost complete destruction of heavy populations of winter eggs of the European red mite by *H. faurei* in some outlying sour cherry orchards in 1950 (personal communication).

#### *Stethorus punctillum* Weise

An account of the importance of *S. punctillum* in the control of phytophagous mites in peach orchards has been published (Putman, 1955). The need of a relatively high density of prey for successful reproduction imposes a limit to its effectiveness against the European red mite, but by attacking the concentrations of first-generation mites on the lower leaves in the spring and the declining population, including the winter eggs, after its crash in late July or August, it was once one of the more influential predators. It was probably even more important in the control of the two-spotted spider mite, but had little or no effect against the clover mite. At present *S. punctillum* is relatively scarce throughout the intensive orchard areas of the Peninsula as a result of general spraying with DDT and parathion.

#### CHRYSOPIDS

The larvae of *Chrysopa rufilabris* Burm. and *C. plorabunda* Fitch feed readily on all stages of the European red mite and the two-spotted spider mite. Both species were reared from egg to maturity on European red mites alone.

The life-histories of these species and their occurrence in local peach orchards from 1931 to 1935 were given by Putman (1932, 1937); at that time *C. rufilabris* was predominant. During the past few years their positions have been reversed, owing to the susceptibility of *C. rufilabris* and the tolerance of *C. plorabunda* to DDT as described elsewhere (Putman, 1956).

It was difficult to compare the over-all abundance of chrysopids in the period from 1931 to 1935 with that from 1947 to 1955 because of great variation among years and orchards, but they have been at least as abundant and sometimes more so during the recent period. The decrease of *C. rufilabris* has thus been compensated by an increase of *C. plorabunda*, probably due to the plentiful food supply afforded by mite infestations. However, *C. plorabunda* has shown no tendency toward yearly increasing populations even in orchards with heavy annual infestations of European red mite. The lack in peach orchards of suitable food for the adults (Putman, 1937), and their need to seek hibernation sites outside the orchard, are probably among the more important population-limiting factors.

On trees that were not sprayed with insecticides the larvae of *C. rufilabris* usually reached maximum numbers in July and those of *C. plorabunda* in August, although both species may occur from June to October. A combined population of one larva per 200 leaves was exceptionally high, but one per 500 leaves was frequently present in July and August in both DDT-sprayed and unsprayed plots. Such small numbers are partly compensated by the activity and high prey consumption of the larvae, as shown by Fleshner (1950) for the closely related *C. californica* Coq. which preys upon the citrus red mite, *Paratetranychus citri* McGregor. However, experience in different orchards and seasons has shown that chrysopids alone even at their greatest density, are quite incapable of producing any noticeable effect on heavy infestations of the European red mite, which may exceed 100 mites per leaf at their peak. Against low endemic populations of the mite chrysopids may have a relatively much greater influence.

### GENERAL DISCUSSION

The difficulty of investigating the role of natural enemies of phytophagous mites in peach orchards under present conditions must be emphasized. In the main peach-growing areas of the Niagara Peninsula probably 80 per cent of the land is occupied by orchards or vineyards, nearly all of them sprayed annually since 1948 or earlier with DDT or, more recently, parathion. Neglected orchards are non-existent because of the short life of uncared-for peach trees and the high value of the land. Non-sprayed plots, or entire orchards, are thus oases in a desert of sprayed vegetation on which most predators have been destroyed. The general reduction in all orchards of *S. punctillum*, *H. faurei*, and *C. rufilabris* following the use of DDT in most of them has already been mentioned, and other less important predators have probably been likewise reduced.

Until 1952, the only orchards available for study were commercial ones; the owners could be persuaded to omit insecticides from some plots for three or four years but they insisted that sulphur be applied for brown rot control. Since 1952 some small orchards have been under our complete control, but by that time the predators just mentioned had become scarce throughout the district. The full complement of predators has therefore never been seen at work in a non-sprayed orchard, but examples of the effectiveness of some species were observed in 1947 and 1948. When the initial spring population of the European red mite was high, as a result of a large carry-over of winter eggs, predators were never able to suppress population growth before the foliage was severely injured, usually in July. A population of 20 mites per 100 leaves at mid June frequently produced such an infestation, and one of 100 mites per 100 leaves invariably did so. It is true that most such infestations have occurred in plots where pesticides likely to reduce the predators were used the previous season, but consideration of the size of the spring populations of the predators and their observed rate of increase shows that they are very unlikely to produce early-season control of the mite. After the crash of a large population of the European red mite, usually by early August, predators may become very effective against the residual population that produces the winter eggs. Where pesticides do not interfere, the numbers of phytoseiid mites and

*H. faurei* usually approach maxima during August shortly after the crash, and *S. punctillum* may be still common at that time. The two latter species also continue to feed upon the winter eggs until late in the season. An example of extensive destruction of the eggs was given by Putman (1955); in a plot sprayed with sulphur alone, only 3.2 per cent of the eggs were still intact in December, 1948, whereas 48.4 and 48.6 per cent were intact in DDT-sprayed plots in the same orchard. In this case *S. punctillum* was largely responsible, but in some other orchards *H. faurei* destroyed a large part of the eggs.

More recently it has been possible to study some small orchards of three to four acres that received fungicides only or were left partly unsprayed. One such orchard was maintained from 1952 to 1954, and two others from 1953 and 1954 respectively to the present (1956). Despite the general reduction of the more mobile predators just mentioned, populations of the European red mite have remained very low, well below the economic level, in these orchards. All predators were generally scarce and in some plots practically absent. The results from these orchards raise the question whether predators are truly the factors controlling the mite population, and further, question the assumption that DDT promotes increase of the mite through destruction of these predators. It may be that special conditions in these particular orchards, for example, nutrition of the trees, have made them unsuitable for the mite, and that they are not typical of peach orchards in general, but much further work is needed before any definite conclusions can be reached. In the meantime it may be said that the present investigations have neither proved nor disproved the thesis of Hueck *et al.* (1952) that DDT favours increase of the European red mite through direct physiological effect.

The occurrence of the two-spotted spider mite in discrete colonies beneath a web makes this species more susceptible to predation. Predators such as *S. punctillum*, phytoseiid mites, and thrips penetrate the web and remain beneath it until the colony is cleaned out. During 1931 to 1935, when large samples of leaves were examined directly on the trees, a large portion of the colonies showed evidence of predation either by presence of the predators or by the remains of dead mites in exterminated colonies. During this period infestations of the mite never progressed beyond the incipient stage. There has been no opportunity to observe predators at work on severe infestations because the latter appeared only in plots heavily sprayed with DDT.

Despite the apparent effectiveness of predators in the control of the two-spotted spider mite, weather factors are at least as important. This was indicated by parallel fluctuations of the mite populations in DDT-sprayed and hence relatively predator-free orchards several miles apart; very intense infestations in one year sometimes failed to appear the following year.

Certain predators, as mentioned previously, have been seen attacking the peach silver mite and larvae of the clover mite, but nothing is known about their effects on the prey populations. During 1931 to 1935 unidentified phytoseiids sometimes became very abundant on trees heavily infested with the peach silver mite but practically free of other prey. No corresponding increase of predators has followed a build-up of the clover mite.

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### DISCUSSION

J. A. HALL. In our orchards the decline of European red mite over the past five years has been very regular at about the 10th of August, regardless of differing seasonal or foliage conditions.

P. J. CHAPMAN. In regard to the midsummer decline in European red mite populations, this is attributed to a basic physiological seasonal change in the physiology of the trees primarily and may be unrelated to the activity of natural enemies.





# Organisation de la Lutte biologique en France et Résultats obtenus dans l'Utilisation des Agents pathogènes

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En France, comme ailleurs dans le Monde, les conditions créées par la meilleure connaissance biologique des insectes nuisibles et par les progrès de la toxicologie et de la lutte chimique ont amené l'I.N.R.A. et son département d'Entomologie agricole à constituer une Unité Spécialisée de la Lutte Biologique.

Cette Unité comprend deux laboratoires, l'un à Antibes spécialement orienté vers l'étude des insectes Entomophages et qui sera dirigé à partir de 1957 par le Dr Biliotti, l'autre à La Minière près Versailles, spécialement orienté vers l'utilisation des micro-organismes pathogènes pour les insectes.

Les deux laboratoires travaillent selon des méthodes analogues, dont les principes sont liés au développement simultané des deux catégories d'études suivantes:

1°. Etudes fondamentales sur les biocoenoses et sur les facteurs naturels de limitation des populations d'insectes phytophages se rapportant surtout à l'étude approfondie d'un petit nombre de ces facteurs naturels plutôt qu'à l'étude extensive du peuplement d'un milieu. Par exemple E. Biliotti a développé l'étude expérimentale des facteurs de la spécificité parasitaire de certaines espèces de Tachinaires qui font l'objet d'une communication à ce Congrès. A un autre point de vue, j'ai moi-même plus spécialement étudié les facteurs de fécondité chez le Doryphore (Grison 1952) et également d'une manière préliminaire chez certains Lépidoptères (Grison 1956).

Une des conséquences de ces études a été de mettre en évidence certaines préoccupations et recommandations se rapportant à la préservation de faunes utiles lors des traitements insecticides (Grison et Biliotti, 1951 et 1954).

2°. Etudes sur les applications de la lutte biologique.

a) Le laboratoire d'Antibes se préoccupe plus spécialement des élevages et de l'utilisation des insectes auxiliaires (*Novius cardinalis*, *Cryptolaemus montrouzieri*, *Aphelinus mali* et *Macrocentrus ancylicivorus*); il a pris en charge également l'élevage et les études écologiques sur l'acclimatation de *Prospaltella perniciosi* dans le cadre d'un programme de collaboration internationale de Lutte Biologique.

b) Le laboratoire de La Minière est plus spécialement orienté vers l'utilisation des agents pathogènes des insectes comme méthode de lutte biologique en connection avec l'Institut Pasteur pour ce qui concerne les études bactériologiques proprement dites et le laboratoire du Dr Vago à Alès pour ce qui concerne l'histopathologie et les études de pathogénèse.

## UTILISATION DES AGENTS PATHOGENES ET OBSERVATIONS ECOLOGIQUES

Il ne semble pas nécessaire de procéder à un rappel historique de la contribution qui a été apportée dans ce domaine, par certains chercheurs français de l'I.N.R.A. (Paillot 1933) et de l'Institut Pasteur (Metchnikov et Chorine 1930).

Nous résumons brièvement les principaux résultats obtenus ces dernières années par l'utilisation de bactéries et de virus contre la Piéride du Chou ainsi que cela est rapporté ailleurs (*in* "Entomophaga"). Auparavant, nous montrons dans une série de clichés comment nous mettrons en évidence au cours de nos études écologiques l'importance et le rôle des maladies épizootiques des insectes phytophages dans la limitation de la prolifération de ces derniers.

Nous avons pris comme exemple les observations faites dans les différents biotopes où se développe normalement le *Bombyx cul brun*, *Euproctis chrysorrhoea* (Don.):

- cas des garennes à *Quercus* sp. d'Ile de France;
- cas des dunes à *Hippophae rhamnoides* du littoral de la Mer du Nord;
- cas des maquis à *Arbutus unedo* de la région méditerranéenne;
- cas des peuplements de *Castanea sativa* du plateau du Niolo en Corse;
- cas des plantations d'alignement d'*Acer pseudoplatanus* dans les Villes (Ville de Paris).

En 1954, alors que la gradation avait atteint son point culminant dans les maquis d'Arbousiers (région de Béziers, Iles d'Hyères) et que le feuillage de ceux-ci était totalement "brouté" par les chenilles de *E. chrysorrhoea*, une brutale épizootie à polyédrose et à mycose s'est manifestée et a anéanti la population en une saison.

C'est un cas typique d'intervention brutale des agents pathogènes dans la rupture d'une "gradation". Speare et Colley (1912) avaient songé à multiplier et à utiliser le champignon *Entomophthora aulicae* (Reich.) aux U.S.A.

Dans un autre cas et un autre biotope (gradation de *Lymantria dispar* en suberaie — *Quercus suber* —) cette rupture a été provoquée par un Insecte prédateur, *Calosoma sycophanta* (Grisson 1955) qui avait fait l'objet d'introduction et d'acclimatation aux U.S.A. (Burgess 1911).

Citons encore les observations faites sur la fréquence relative de la Mouche Tachinaire *Cyzenis albicans* dans des biotopes climatiques différents à l'occasion des études menées sur la Cheimatobie, *Operophtera brumata* (L.) (Grisson et Silvestre de Sacy 1948, Arnoux 1951).

A Versailles, dans les plantations d'alignement de Tilleuls, 30 à 40 p. 100 des chenilles sont généralement parasitées par cette Tachinaire, tandis qu'à Bernay en verger de Pommiers, le taux de parasitisme par cette même espèce n'excède pas 5 p. 100.

La faune d'un milieu n'est donc pas envisagée sous l'aspect d'un inventaire de peuplement de ce milieu sans que soient définis les liens d'interdépendance des espèces entre elles, en d'autres termes, il ne nous semble pas opportun de collationner des espèces disparates, abondantes ou non, dont l'éthologie serait peu ou mal connue et le statut écologique non précisé.

Du point de vue agronomique comme du point de vue de la biologie générale, il est plus urgent de rassembler autour de l'espèce fondamentale toutes celles qui vivent en concurrence ou à ses dépens. En étudiant ainsi la Processionnaire du Chêne, non seulement des indications biologiques utiles et originales ont été recueillies sur certains entomophages mais des "relations d'interdépendance" et des "degrés de fidélité" ont été établis au sein de ce type de biocénose (Biliotti 1952).

Le problème est identique en ce qui concerne les phénomènes de régulation d'infestations de ravageurs par les agents pathogènes (Grisson et Vago 1953) et il serait heureux que les études biocœnotiques aboutissent à canaliser l'ensemble des forces utiles de la nature de telle sorte qu'elles se complètent constamment sans jamais se concurrencer pour le plus grand profit de l'Homme.

## UTILISATION PRATIQUE DES AGENTS PATHOGENES ET APPLICATIONS EN PLEIN CHAMP

Nous avons précisé l'un des buts pour lesquels le Laboratoire de La Minière (près Versailles) a été créé et se rapportant à l'utilisation des germes pathogènes comme méthode de lutte biologique et pour laquelle il a été tenu compte très largement et très utilement des résultats déjà obtenus aux U.S.A. et au Canada (le traité de E. A. Steinhilber 1949 donne une bibliographie détaillée à ce sujet).

Si les recherches fondamentales de Biocœnotique et de Pathologie peuvent se poursuivre sur les Insectes les plus variés, nuisibles ou non, par contre les mises au point techniques doivent porter seulement sur un nombre restreint d'espèces judicieusement choisies du point de vue de leur intérêt économique.

Nous limiterons nos exemples à ceux qui se rapportent aux applications faites sur *Pieris brassicae* (L.) et nous en résumerons les résultats.

1°. CAS DU TRAITEMENT BACTÉRIEN (Lemoigne *et al.* 1956) : Une souche de *Bacillus thuringiensis* BERLINER dite "Anduze" (Delaporte et Béguin 1956) et isolée en 1952 dans une magnanerie des Cévennes a été cultivée et préparée en vue de son utilisation comme moyen de lutte bactériologique contre la Piéride du Chou, *Pieris brassicae* (L.).

Cette souche, sporogène et cristallogène (Angus 1954), est très pathogène vis-à-vis de certaines larves de Lépidoptères et beaucoup plus virulente que d'autres souches de *B. thuringiensis* auxquelles elle a été comparée.

Elle a été multipliée en culture sur milieu liquide de pH = 7, soumise à l'agitation à 30°C pendant environ 20 heures. La masse de spores obtenue a été recueillie après centrifugation et remise en suspension dans un petit volume d'eau.

Ainsi préparée et conservée en chambre froide à + 4°C, l'activité pathogène de la suspension de spores reste intacte pendant plusieurs mois. Par ailleurs, le maintien de la virulence de la souche a été contrôlé après de nombreux repiquages sur différents milieux.

La suspension de spores est utilisée, tant au laboratoire qu'en plein air, après dilution dans l'eau ordinaire pour ramener la concentration à 100 ou 200 millions de spores par centimètre cube. A cette concentration, on obtient au laboratoire, par la méthode d'essais au rameau, une mortalité totale des chenilles de Piéride du Chou de tous stades plus ou moins rapidement mais au maximum dans un délai de quinze jours à une température de 18°C-20°C. Des constatations analogues ont été faites dans des essais parcellaires en plein air.

Enfin, en application expérimentale de plein champ, sur une parcelle de 5 ares et avec un appareil de pulvérisation donnant 3 à 4 kilogrammes de pression, nous avons obtenu une efficacité pratique remarquable de la suspension de spores de *B. thuringiensis* souche "Anduze": la culture de chou-fleur a été protégée contre la Piéride du Chou d'une manière plus satisfaisante qu'avec un traitement insecticide classique, ce qui confirme les résultats obtenus par Steinhaus (1951) et Tanada (1953).

2°. CAS DU TRAITEMENT AVEC GERME VIRUSAL: L'utilisation des corps d'inclusion contenant les virus proprement dits est d'application beaucoup plus récente (Bird 1950, Steinhaus et Thompson 1950, Franz et Niklas 1954, Tanada 1956 . . .).

Les "granuloses" sont particulièrement intéressantes à ce point de vue et nous nous sommes adressé à celle qui a été décrite par Vago, Lépine et Croissant (1955) et que nous avons rencontrée dans nos élevages de *Pieris brassicae*. Les cadavres recueillis à la suite d'une épizootie ont été utilisés à préparer une suspension virulente selon la technique décrite par Bird (1952) pour les suspensions de polyèdres de *Neodiprion sertifer* (Geoffr.). Une partie du stock fut employée pour renouveler artificiellement en élevage une épizootie de multiplication de germes virulents qui réussit parfaitement.

Nous étions alors en mesure de tenter l'expérience de plein champ qui fut réalisée à La Crau (Var) sur culture de Choux-fleurs (Biliotti, Grison, Martouret 1956). L'application a été faite le 1er décembre 1955 sur des parcelles de un are infestées d'une manière hétérogène par des chenilles des 3ème au 5ème stades larvaires et la dispersion a été réalisée dans les conditions de la pratique agricole.

Dans la parcelle témoin, toutes les chenilles, après avoir eu une activité intense et une croissance normale avaient quitté les plantes à la date du 16 décembre pour aller se nymphoser.

Sur les parcelles traitées, et dans la semaine qui suivit l'opération, nous avons pu nous rendre compte que la croissance était considérablement ralentie tandis que l'activité des chenilles caractérisée à la fois par la capacité réflexogène et par la consommation était très réduite; puis brusquement à partir du 22 décembre, soit trois semaines après

la date du traitement, les symptômes de la granulose typique apparurent<sup>1</sup> et l'épizootie fut totale et foudroyante entre le 22 et le 31 décembre.

Dans le cas d'une chenille qui, comme la Piéride du Chou, effectue une migration obligatoire au moment de la nymphose, il peut y avoir transmission éventuelle des virus par les survivantes au moment de ces déplacements. Nous avons également envisagé d'étudier la vitalité de la descendance de papillons issus de ces survivantes.

Dans ce but, nous avons récolté quelques dizaines de nymphes provenant de chenilles ayant subi le traitement et nous les avons placées dans les conditions d'élevage au Laboratoire décrit ailleurs.

Les imagos sont éclos et ont pondu normalement. Par contre une très forte proportion de chenilles du 1er stade fut décimée par la maladie, laquelle fut diagnostiquée par la reconnaissance des corps d'inclusion dans les cadavres.

Ce phénomène présente un double intérêt: du point de vue pathologique il mérite d'être analysé par le spécialiste; du point de vue écologique, ce qui nous importe ici, il peut constituer la garantie d'une destruction quasi-totale d'une population de Piérides même à la suite d'un traitement tardif ou lorsqu'une partie des chenilles parviennent à la nymphose.

3.° CONCLUSIONS: Nous avons, après Steinhaus, posé (Grisson 1956) quelques-unes des questions auxquelles l'entomologiste, en plein accord avec le pathologiste, devrait pouvoir répondre avant d'envisager l'utilisation pratique des germes pathogènes d'insectes comme méthode de lutte biologique.

Nous devons nécessairement nous limiter actuellement à un nombre de cas restreints et se rapportant au choix judicieux de l'association "parasite-hôte".

Les épreuves d'efficacité au laboratoire qui doivent précéder d'une manière systématique les applications de plein champ ont fait l'objet d'une mise au point approfondie au Laboratoire de La Minière (Burgerjon 1956).

Les conditions écologiques des applications doivent être prises en grande considération comme l'a indiqué Steinhaus et du fait de nos connaissances insuffisantes dans ce domaine certains traitements peuvent être faits empiriquement. Au moins ne faut-il pas négliger les limites d'utilisation des germes pathogènes et doit-on tenir compte de certains facteurs dans l'interprétation des résultats.

Parmi ces facteurs, nous accordons une importance particulière aux modalités d'action toxique des germes dont quelques-unes ont été bien mises en évidence par Angus et Heimpel (1955, 1956); ainsi qu'au rôle des microorganismes "opportunistes", comme les appelle Steinhaus, et qui sont susceptibles de constituer, avec le germe dispersé artificiellement, des "entités morbides" récemment étudiées d'une manière approfondie par Vago (1954, 1956).

Ces préoccupations ne sont pas éloignées de celles des toxicologues lorsque ceux-ci tendent à proposer une utilisation aussi rationnelle que possible des insecticides chimiques dont les mérites pour l'Economie agricole sont incontestables; mais le souci de préserver puis de créer des équilibres biologiques bénéfiques pour l'Homme reste la meilleure justification des études de biocénologie et de lutte biologique.

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<sup>1</sup> Quelques individus de *Pieris rapae* (L.) présents dans la culture furent retrouvés morts au cours des contrôles et ils présentaient les symptômes d'une granulose.



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## DISCUSSION

J. VAN DEN BRANDE. Have you been importing some insect parasites in France? Being from Belgium, it may be of importance for my country.

P. GRISON. Two problems have been under study in Antibes: *Macrocentrus ancyli-vorus*, imported by J. Ghesquiere but which will not be released until ecological experiments have been carried out, and *Prospeltella perniciosi* and *P. berlesi*; the first against the San José scale will be the object of ecological experiments in France (Antibes) and in Germany (Stuttgart).



# Protozoan Diseases in Insect Control

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## ABSTRACT

Of the great number of Protozoa living in insects only three groups are of interest in biological control: Schizogregarina, Coccidia and Microsporidia. Schizogregarina may be important controlling factors in populations of stored grain insects. The Microsporidia are the most important protozoa associated with insects. Infection occurs *per os* with the food. Although infection may result from the ingestion of small doses of spores, the course and degree of infection is dependent upon the size of the dose. In lethal infections, death of the host population occurs over a long period; the mortality curve can be divided into three phases on the basis of rate and most of the individual hosts die in the middle phase. No cellular or humoral resistance responses of the hosts to infection have been demonstrated. Most Microsporidia are more or less specific parasites on a narrow range of host species; susceptible hosts are related ecologically or nutritionally rather than taxonomically. Within the host, Microsporidia attack specific organs and tissues. Transmission of the infections occurs by contamination of the food by excreta and by decomposing hosts, by cannibalism and by predation. Hereditary transmission occurs in a few cases only. The spores are resistant to a variety of unfavourable conditions. Experimental infection of caterpillar populations with resulting mortality of 90-100% has been secured with microsporidial disease of the fat body, by spraying spores over the host-infested area or just in spots or strips of the area. Although transovarial transmission of these infections has not occurred, the disease may persist from one season to another if the host larvae hibernate.

There is very little known about the influence of protozoan diseases upon the natural populations of insects. The role of the microsporidia in natural control of insects has been in general underestimated. This is due to the peculiarities of the infections and to the lack of the necessary knowledge by the insect ecologists. An insect attacked by a protozoan disease is an easy prey for the predators. It may lie motionless for many days before death without bacterial decomposition on leaves. In our field experiments caterpillars with a microsporidian infection have been consumed by predators just a day after the first signs of the disease. The caterpillars with bacterial or polyhedral infection on the other hand may be found on leaves for many days, even after their death. The mentioned lack of knowledge of protozoan diseases by ecologists results in "clinical" diagnoses of diseases only. With the exception of wilt and mycoses all other cases of mortality are usually listed as "natural mortality" though it is evident that the natural mortality occurs only in old imagos after oviposition. The role of protozoa in the regulation of natural populations is indicated by the increasing number of new discoveries of these parasites in recent years.

Schizogregarina, Coccidia and Haplosporidia causing diseases of insects will not be referred to here however interesting these groups are.

Of approximately 250 known microsporidia, more than 150 species are parasites of insects. In Czechoslovakia we have found more than 56 species so far and 29 of these were new species. In all cases the microsporidia have been found to cause diseases resulting, sooner or later, in the death of the host. In microsporidia the infection is by means of spores which enter the digestive tube of the host with the food. Only occasionally hymenopterous parasites are vectors of a percutaneous infection.

The phenomenon of phagocytosis is rare in microsporidial infections and its occurrence is mostly connected with other anomalies in the host-parasite relation. So *Nosema baetis* causes a hyperplasia of the infected cells of the fat body in Ephemerids. The hyperplasia is caused by a tissue-specific metabolite of the parasite having a localised effect, without ability of penetration of the cell wall (Weiser, 1956). In this case phagocytosis also has been observed. Schizonts phagocytised by leucocytes proceed in their development without hyperplasia of the nucleus and fill the leucocyte,

forming a pseudocyst. Besides phagocytosis giant cells are also formed. Groups of leucocytes are agglutinated around greater groups of spores, forming a cyst in which the spores are destroyed. But neither the phagocytosis nor the formation of giant cells may cause the suppression of the parasite. Phagocytosis starting at the beginning of the infection diminishes gradually and has no influence on the result of the infection. No resistance is acquired and consequently the infection with Microsporidia develops with great regularity, mostly without any influence from the environment.

The specificity to a given host and tissue has been accepted generally as one of the criteria for taxonomy of microsporidia until recently. The experiments with *N. apis* and *N. bombycis* or with *N. destructor* (Steinhaus) have shown however, that microsporidia are infectious for more than one host species in most cases. This broader host-range may be characteristic in a taxonomic sense for a given parasite species (Weiser, 1956). If two microsporidia have one host in common, it does not follow that the other hosts of both parasites are common too. We have found 4 species infecting *Lymantria dispar* L. But only three of them are infective to *Nygma phaeorrhoea* Don. and only two to *Hyphantria cunea* Drury. On the other hand microsporidia infective for *H. cunea* or *N. phaeorrhoea* are not infective for *L. dispar*. The tissue-specificity is more pronounced than host specificity. Most species infect only one tissue in numerous hosts. In other species a succession of infected tissues occurs. So, in *N. otiorrhynchi*, malpighian tubes are infected at first, then the fat body and subsequently other tissues including the gonads. In the selection of host tissues, the microsporidia bears no relation to the morphological origin of the tissues. So, in *Nosema muscularis*, the parasite of *L. dispar*, the muscle tissue of the gut is infected but the musculature of the body remain intact. The matrix of the tracheae is infected, but the analogous hypodermis is not parasitised and similarly, the epithelium of the malpighian tubes is parasitised but the gut-epithelium is without infection (Weiser, 1957).

The transmission of microsporidia from host to host is mostly accomplished by the contamination of the food with faeces and the remains of decayed bodies of infected specimens, by cannibalism or by transovarial and pseudohereditary infection. Only in exceptional cases a true transovarial infection is accomplished. As a further way of transmission from host to host the percutaneous transmission by stings of entomophagous insects must be taken into account (Allen, 1954; Blunck, 1954, *et al.*). The infective material from dead insects is liberated by decomposition of their bodies by sun and rain, and in most cases with the assistance of predacious arthropods such as mites (*Tyrophagus noxius* a.o.), ants (*Formica rufa* a.o.), bugs and beetles (*Calosoma*, *Xylodrepa* a.o.) (Weiser, 1957b). The spores are liberated from gnawed remains of insects or from the faeces of non-susceptible insects, the digestive tube of which they pass through without being altered.

There are many references on the resistance of spores of *N. apis* and *N. bombycis*, most of which differ according to the experimental methods used. Our own experiments with *Thelohania hyphantriae*, *N. lymantriae*, *N. muscularis* and *T. similis* show that the resistance of the spores of these microsporidia may be evaluated as follows: Isolated spores smeared and dried on microscopic slides at laboratory temperature are still viable after one month and at a constant temperature of 0°C. after two to three months. On soil, or in the soil, the spores live more than 12 months. In water at 20°C. the spores are viable after three to four months, and in some cases *T. similis* after one year. At 0°C. the spores in water suspension are still viable after 13 months. In dead insects at 80% to 90% relative humidity the spores are viable after 13 months but in dried specimens only two months. Water is of fundamental importance for viability of the spores.

Temperatures of 20° to 25°C. are most suitable for the development of the microsporidia in insects. At lower temperatures the development is slower, at higher it is faster. At about 10°C. development stops and in this condition are schizonts and spores of the microsporidia viable for more than five months, withstanding freezing up to -29°C. for more than a week. With the temperature rising above 10°C. the development of the disease is resumed. Spores at a temperature of -20°C. die after six days, at -40°C. after 24 hours. The upper limit of variability is 65-70°C. the spores dying after five minutes of exposure. At 60°C. the spores are killed after 20 minutes

at 40°C. after 30 minutes. Allen found a temperature of 70°C. for 20 minutes to be non-fatal for *N. destructor*. A temperature of 48°C. used in the sterilization of the eggs of *Bombyx mori* (Ovanesjan, 1954) does not kill the spores of *N. bombycis*. It seems probable that this temperature is effective only for the vegetative stages of the parasite, the spores resting in the egg having in the succeeding caterpillar period no possibility of being opened by digestive fluids and consequently the infection is avoided. Allen (1954) used the same method for the sterilization of *N. destructor*.

Microsporidia are members of normal biocenoses. In most cases there is a group of hosts among which the infection circulates. These are species living in the same biotope, with the same requirements or with the same host plant. Alimentary relations are more important than the phylogenetical ones. One or more members of this host-chain becomes the reservoir of the infection for other host species, living in other biotops, which are susceptible to the infection, but having no direct connection with the first group. Thus in the fall webworm, *H. cunea*, which has been brought to middle Europe recently, two microsporidian infections have been found and also some bacterial and fungous infections. As these infections were first found several years after the first appearance of the pest, it seemed probable, that they have not been imported from America along with the host. And they have been found later as natural infections in *N. phaeorrhoea* and *Aporia crataegi* L.

With the attacks of predators on the infected insects, the infective material from the organs of the insects is liberated and spread with faeces and the remnants of the dead bodies. The biotops tend to reduce the frequency of the microsporidian material. The dead insects fall to the soil, are swallowed by predators, and the infected leaves fall to the earth. So the level of the infective material in the biotope is continuously diminished to a certain level of stabilization, corresponding to the population density of the host, the number of predators and to a degree depending on the site of infection and the resistance of the spores.

All infections of an acute character, manifested by physiological symptoms, stimulate attack by predators. Chronic cases without manifest symptoms are not so greatly affected and their frequency in the population is much greater. As examples of these acute infections we see *Thelohania legeri* in *Anopheles*: frequency 0.5-10%, *T. opacita* in *Aedes*: frequency 1-7%, *T. varians* in *Simulium* in 2-5%, *T. hyphantriae* in *Hyphantria* 0.5-1%, in *Malacosoma* 3-5%, in *Nygma* 1-2%. *T. similis* in *N. phaeorrhoea* in 1-5%. On the other hand in chronic infections: *Pérezia pyraustae* in *Pyrausta nubilalis* Hbn. in 30%, *Nosema carpocapsae* in *C. pomonella* L. in 30-40%, *Pérezia mesnili* in *Pieris brassicae* L. in 30-70% of cases and *N. apis* in *Apis mellifica* L. in 50-60% cases. When the hosts with acute infections are protected against the attack of the predators, the frequency of infection rises immediately. E.g. *N. otiorrhynchi* in *Otiorrhynchus ligustici* F. from 20-75%, *Nosema steinhausi* in *Tyrophagus noxius* from 10-80%, *T. hyphantriae* in *Hyphantria* from 0.5-80% and 98% respectively.

In the infections of insects by microsporidia in the first days of the infection, the rate of attack by septicaemia increases. It has been found that the planonts on their way through the gut epithelium bring bacteria to the tissues of the host and there the septicaemia is initiated. In the period of these first septicaemias no spores of the microsporidian are formed and in smear preparations from dead insects the real cause of death, viz. infection with microsporidia, is not diagnosed.

In recent years we have pursued the fate of an infection with different microsporidia in more than 25,000 insects in the laboratory. In field experiments we used *T. hyphantriae*, *N. lymantriae*, *N. muscularis* and *T. similis* combatting *H. cunea*, *N. phaeorrhoea* and *L. dispar* (Weiser, 1957b; Weiser, Veber, 1957). More than 30,000 of *Hyphantria* caterpillars and more than 10,000 caterpillars of *N. phaeorrhoea* were treated with spore suspensions. About 15,000 caterpillars of *N. phaeorrhoea* were sprayed with spores before hibernation. In all cases we had distinctly positive results; all specimens coming in contact with contaminated food were infected and about 80% in the larval stage died of the infection. The rest pupated and only 3% of the infected pupae emerged. The microsporidia infect the host with a standard virulence without influence by weather or feeding conditions of the host. The course of infection was in all cases



about the same. The first insects died from the 5th to 7th day of the incubation at 21°C. Changes in temperature result in changing the time necessary for incubation.

The incubation changes from three days at 28°C. and 14 days at 15°C. to several months in the case of hibernation. The infective dose is low, 100 to 1,000 spores. Doses below this level induced long-lasting infections, great doses caused acute infections, excessive doses quickly end in a septicaemia due to extensive perforation of the gut. After one week of incubation, the infection is usually well under way.

For the cultivation of microsporidia insects are used in a stage in which the organ infected has reached its greatest volume. This is mostly the last instar, larval stage within more than 14 days before pupation. This period is much prolonged by the infection and the infected insects pupate with much delay. From the different host-species those with the greatest effect of spores is used. There is no difference in the virulence of the spores from different host-species.

If uncontaminated spores are needed or if we wish to divide a mixed infection of two microsporidia attacking different organs of the same host, infected organs are dissected from living insects and used for the infection. To obtain material from the infections of the gut the intestinal tract is drawn out from the decapitated body. The infected fat body is rolled out after extraction of the gut by means of a glass rod. In isolations of larger masses of spores a Waring Blendor is used, one sample requires about 30 to 100 caterpillars and 100 ml. of water. In intestinal infections also the infected faeces are sampled. The spore suspension is filtered with a double gauze, retaining hairs, fragments of the tissues and remains of the food. The concentrated suspension may be preserved in an ice box for more than two months without deterioration, in some cases remaining active for more than ten months. Addition of penicillin and streptomycin to the suspensions reduced the initial septicaemiae in treated insects. Dead, desiccated caterpillars are not suitable for long preservation. For application different sprayers are used. One of the cheapest for small samples is the fixative-sprayer. For greater volumes of suspensions we use different compression sprayers. For better adhesion, molasses (2-5%), milk, clay or casein is added. The adjuvants may have in some cases repellent effects on insects concerned. We use suspensions of spores in water containing 1,000 to 3,000 spores in 1 microliter. With 1 ml. of this suspension about 1 m<sup>2</sup> of leaf area may be sprayed. The determination of the density of the suspension is made by counting the spores in a counting chamber for leucocytes. In small plants, the whole plant is sprayed; in bigger trees spot-spraying of a part of the branches and leaves is used.

Mixed infections of insects by two or more species of microsporidia does not give better results than pure infections. The incubation is not shorter and the result is identical with that of the more acute of either infection. In some cases syndromes of two or more infections are produced and the mixed infection may be transmitted by the same vector or infective material. One of these cases is the infection of *L. dispar* with *N. muscularis* and *N. lymantriae* (Weiser, 1957a).

We have found during our research that whereas the infections are specific in spite of the infectivity to different hosts, this characteristic could be changed in some cases (Weiser, 1957a). It has been found in experimental infections with increasing doses that *N. lymantriae* living in the fat body of *L. dispar* is not infectious for *N. phaeorrhoea*. In *N. phaeorrhoea* another microsporidian, *T. similis*, has been revealed in the fat body, which is infective for both, *Nygma* and *Lymantria*. Now, if we use mixed spores of *N. lymantriae* and *T. similis* for the infection of *N. phaeorrhoea*, we get a mixed infection with both microsporidia in the fat body of the host. In this case, *T. similis* acted as a conditioning and protecting factor enabling the development of the other species inside the unusual host. In other cases *T. hyphantriae*, *P. schubergi*, *N. lymantriae*, *N. muscularis*) this phenomenon has not been found.

A very important factor in the biological control of insects is the compatibility of the natural controlling agents with insecticides. In a former paper (Weiser, 1951), it has been demonstrated that the interference of the insecticide with disease caused a rise in mortality about ten times greater than the controls. But for the further development of the infection in the population, the decrease in population density caused by

insecticides is fatal. Not only is the mortality of the insects (especially infected specimens) increased by insecticides, but in the dying insects the infection is not well developed and in most cases the development of the parasite does not surpass the stage of schizonts, so that the distribution by predators cannot start. It is, therefore, better to use the microsporidia without the application of insecticides. It has been demonstrated that the advancement of a pest into new areas is accomplished by a population lacking infection and that the diseases are found in most cases only in the old foci of the pest. So it seems better to use insecticides only for the control at the periphery of the infestation to produce there the best possible control and to use biological weapons for the inside of the area. In some cases the insecticide used may kill the predators and entomophagous insects resulting in a more virile, uninfected population of the pest.

Our investigations of the use of microsporidia in biological control of insects have shown them to have practical application. We have obtained good results in one-season experiments. But the hope of achieving longer-lasting results leading to an automatic regulation of the pest population remains a matter for further research. One of the disadvantages of Microsporidia is the impossibility of culturing them on artificial media. On the other hand, unlike bacteria, they do not lose viability and virulence in a short time. Unlike fungi, they do not need any special conditions of humidity and temperance for the infection of the host. We find in each case of microsporidia a standard infectivity, with the whole development of the parasite in the host and good persistence under special conditions.

The use of microsporidia in biological control of insects promises to develop into a valuable tool especially in persistent biocenoses of forests and orchards. The problem of initiating the practice lies only in the choice of a suitable organism.

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### DISCUSSION

J. FRANZ. Would you please give some additional information on the effect of predators and parasites on the spread of microsporidial diseases?

J. WEISER. Predators diminish the percentage of the infected insects in the population so the estimation of the actual frequency of the disease in a population are lower than in fact. But the spores are not lost for the biocoenose, they are only transported to lower "flats", on and in the soil. A biotope must be saturated with spores for a good infestation of the population.

H. BLUNCK. I should be glad to hear more with reference to the influence of humidity on the spores of microsporidia. How long do they remain infected under dry and humid conditions?

J. WEISER. At this time I can only give you the few data mentioned in my paper. Spores in water or wet insects are living after 13 months in a refrigerator at 0°C.; the dried are dead in two months' time.



# The Use of Viruses in the Biological Control of Some Forest Insects

By F. T. BIRD

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## ABSTRACT<sup>1</sup>

The use of viruses in the biological control of insects depends on the virulence of the viruses, habits of their hosts, and the necessary degree of control. Severe epizootics, independent of weather conditions, can be initiated with highly virulent viruses of the European spruce sawfly, *Diprion hercyniae* (Htg.), and of the European pine sawfly, *Neodiprion sertifer* (Geoffr.), simply by spraying aqueous suspensions of the body contents of virus-killed larvae on a few infested trees. Viruses of low virulence have little or no use in biological control although heavy mortality may result when large quantities of the viruses are sprayed directly on trees on which the insects are feeding. Between these two extremes are viruses of varying usefulness. A virus tested against the jack-pine sawfly, *Neodiprion pratti banksianae* Roh., is of doubtful value because of the large amount of virus necessary for control. Preliminary tests of a virus affecting the red-headed pine sawfly, *Neodiprion lecontei* (Fitch.), indicate that the virus will be very useful as a direct spray to control infestations of this insect but it is doubtful whether epizootics can be initiated from small introductions of the virus. Laboratory and field studies are necessary to determine the usefulness of each virus discovered.

<sup>1</sup>Most of this information has been published under the title, "Virus diseases of sawflies", 1955, *Canad. Ent.* 87: 124-127.





# Use of Fungous Diseases in Biological Control of Insects<sup>1</sup>

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## ABSTRACT

*Though epidemics caused by fungous diseases had been known to occur naturally in insect populations, the idea of using fungi for the control of insects was not conceived until after Bail demonstrated in 1861 that a fungous infection could be initiated in insects. This idea became almost world-wide and, from the latter part of the nineteenth century onward, a number of attempts were made to control insects by the artificial distribution of pathogenic fungi. The unsuccessful attempts have outnumbered the successful but fungous diseases have been manipulated to advantage and the method has economic possibilities. In Nova Scotia, Canada, Dustan demonstrated in the 1920's its value in controlling two pests of apple, the European apple sucker and the green apple bug, using species of *Entomophthoraceae*. There are a number of factors that limit the effectiveness of a fungus and that determine the outcome of attempts to use it in control. Some of the more important are weather, population density, micro-habitat of the fungus and host, resistance of the host and virulence of the fungus, saturation point of the fungus, ease of artificial propagation and distribution of the fungus, time of application, and the ability of the fungus to survive and spread in an insect population. Aside from these limiting factors, two other factors must be considered, namely, the economic value of such a control measure and the effect of the fungus on other biological control agents.*

The purpose of this paper is to review past studies on applied insect mycology and to discuss factors that should be considered when entomogenous fungi are utilized for pest control. This subject has been relatively neglected during the past 30 to 40 years and every attempt should be made to correct this situation.

Experimental work in applied insect mycology started during the latter part of the 19th century and flourished during the next 25 to 30 years with varied results. There have been comparatively few attempts since the early 1920's.

A discussion of individual attempts to control insects by the artificial dissemination of entomogenous fungi is not possible in the time available. However, as it appeared important to illustrate in some way the enormous amount of work that has been done in this field in the past, a list of attempts was prepared and copies have been distributed to those persons attending this session<sup>3</sup>. The information is listed under the headings of Host, Fungus, Results, and Country. The results are the conclusions reached from examination of the reports of the different authors who worked with the same species of insect or fungus. The results of the individual authors and a bibliography were not included because of space limitations. The attempts are listed merely as "successful" or "partially successful" because many authors did not support their results by mortality figures and because the validity of some figures was questioned. In some cases it was difficult to arrive at any conclusion as the experiments were poorly planned or reported or were terminated prematurely.

Some 41 attempts on 28 species or groups of insects are listed as successful but few of the fungi listed as successful are in use today. Perhaps this should be an indication that they were in effect unsuccessful, but it is more probable that the majority are not in use as a result of the apparent general belief that artificial distribution would not be beneficial or because the insect ceased to be of economic importance. Others were dropped for no apparent reason.

A lack of understanding of the factors involved has been the main reason for failure. This does not imply that a complete understanding of the many factors would insure successful results. However, many experiments could have been ruled out after

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<sup>3</sup>This list has not been published but will be published at a later date with additions and corrections, a bibliography, remarks, and summaries of the conclusions of individual authors.

preliminary studies to determine if the host and the environment were suitable. In some cases, a better understanding of the factors might have resulted in success through improved methods of handling.

Improper planning has been another reason for failure. In many of the earlier attempts, the fungus material was distributed before an evaluation of its natural importance could be made, and often before the fungus was identified. This made it impossible to determine the mortality caused by the artificially distributed fungus if the fungus was later found to occur naturally.

Poor reporting of results, though not a reason for failure, is quite possibly a reason why some of the experiments are assessed as unsuccessful.

The factors to be considered when experimenting in applied insect mycology are the environment, the host, and the fungus.

The environment is of primary importance as all fungi have certain temperature and moisture requirements. Moisture is a critical factor as spore production and germination will not occur unless the minimum requirements are provided.

The moisture requirements of different species or groups of fungi vary. Some fungi have been found experimentally to require from 95 to 100 per cent relative humidity whereas others require much less. Personal experiences with *Empusa muscae* Cohn in the laboratory have shown that this fungus causes as high a mortality at 50 per cent relative humidity as it does at 80 per cent. The minimum requirement has not been determined.

Temperature is a critical factor also as there are maximum and minimum limits above or below which a fungus ceases to develop. High temperatures are more important than low temperatures. Fungi can survive and some growth will occur at near-freezing temperatures but they are killed very rapidly at temperatures slightly above their optimum. For example, a laboratory infection of *E. muscae* was checked within a day at a temperature of 85°F.

The area in which control is to be attempted should be selected with the above factors in mind. Desert regions, for example, are very unsuitable, and regions with frequent rainfall provide the most favourable conditions. Temperate regions are suitable provided that a favourable humidity is maintained in the insect micro-habitat after heavy rains. The time of application also depends on the prevalence of favourable conditions of temperature and humidity which usually exist after a heavy rainfall.

Environmental factors important in the spread of fungous diseases are wind and rain.

Unfortunately man has little control over the environment, but the humidity of micro-habitats can be influenced to some extent by overhead irrigation or by the planting of intercrops (Fawcett, 1944). Windbreaks have also been helpful (Waterston, 1940).

If environmental conditions are favourable to the development of a fungous epizootic on an insect population factors relating to the insect and fungus may become limiting. These limiting factors are resistance, habits, habitat, and population density.

The portal of entry of a fungous disease is usually through the insect cuticle and thus the first line of insect resistance is at this point. Certain stages of some groups of insects offer considerable resistance to penetration by a fungus because of their heavily sclerotized exoskeleton.

The habits of the insect influence the natural distribution of the fungus. Active insects and insects that congregate favour the local spread of a disease and migrating insects may spread a disease over large areas.

The location and conditions of the micro-habitat will influence the success of a fungus application.

Fungous diseases are dependent on population density but not to the same degree as are insect parasites and predators.

The characteristics of the fungus present a series of limitations. The first requirement of the fungus is its pathogenicity to the insect. The host range may be confined to a very small number of related insects or may include a large number of very different kinds. Similarly there is variation in the virulence of the fungus to the

different species of susceptible insects. The virulence of some fungi may be increased to a certain extent by continued passage through the same species of insect. For example, when an *E. muscae* infection was transferred to *Kellymyia kellyi* (Ald.) from *Cyzenis albicans* (Fall.), the time from exposure to the disease until death was eight days. However, after five transfers on *K. kellyi*, the time decreased to four days.

Fungi display different degrees of parasitism from those that are obligate parasites to those that can exist also as saprophytes. Both facultative saprophytes as well as obligate parasites have been successfully utilized to reduce insect populations. For example, *Entomophthora sphaerosperma* Fres., an obligate parasite, was successfully used against the apple sucker, *Psylla mali* (Schmldb.), in Nova Scotia (Dustan, 1924), and *Nectria diploa* Berk. and Curt., a fungus that can exist as a saprophyte or as a parasite, was successfully used against the Florida red scale, *Chrysomphalus aonidium* (L.) (Watson, 1915).

Other limiting factors are ease and cost of production and application of fungous material. Sufficient material for artificial distribution may be obtained by culturing on artificial media, by exposing healthy insects to the disease, or by collecting large numbers of diseased insects from a field infection. Application of a fungous disease is made by one or more of the following methods: spraying or dusting spores into the microhabitat of the insect; dipping infested vegetation into a suspension of fungous material; or scattering diseased insects, living or dead, over the infested area. Each method has its advantages and disadvantages and their individual use depends partly on the method by which the fungus is produced and partly on the habits and habitat of the insect host.

Fungi may be utilized to control insects with three ends in view: the fungus may be introduced where it does not occur naturally; the fungus may be applied to initiate the disease before it would normally occur; a naturally occurring fungus may be distributed where the saturation point for fungus and insect has not been attained under natural conditions.

The first case could apply to a native or an introduced insect. The same principle is applicable to the introduction of a fungus as to an insect parasite. For example, the introduction of *E. sphaerosperma* into disease-free orchards in Nova Scotia.

Secondly, distribution of this same fungus in orchards where it occurred naturally resulted in initiating the disease about three weeks earlier than it would normally have occurred (Dustan, 1924).

Finally, the distribution of naturally occurring fungi against certain citrus insects in Florida was effective in increasing the mortality of these insects. In this case the amount of fungus naturally present was not sufficient to cause maximum infection under prevailing conditions. That is, the saturation point for fungus and insect had not been reached.

The utilization of entomogenous fungi in the control of insects has its advantages and disadvantages. Their use, if successful, is a relatively inexpensive method of control. Most fungi can be produced in large quantities on simple, inexpensive media and further studies will no doubt provide similar methods for producing the other species. Species that cannot be cultured can be obtained by the collection of infected material in the field or propagated on their hosts in the insectary.

Another advantage is that once the fungus becomes established it may maintain its controlling action over many generations of the host and if conditions are favourable, its effectiveness may increase and, through natural spread, cause widespread epizootics.

Like other biological control agents, entomogenous fungi have little or no effect on other plant or animal life. This is very important because of the increasing danger from insecticidal residues.

An advantage of fungi over insect parasites and predators is that fungi are not affected by most insecticides. Thus, an insecticide can be applied if the insect becomes an immediate threat to the crop without requiring a re-introduction of the fungus. In fact, it might be possible to combine the insecticide and fungus in one application.

The main disadvantage of fungi is their dependence on the environmental conditions for the time of application, development, spread and survival. Another disadvantage is that there is a lag of about a week after application before the disease becomes evident and even longer before it becomes epizootic.

A criticism of the use of entomogenous fungi was reported by Ulyett and Schonken (1940) with regard to *E. sphaerosperma* on *Plutella maculipennis* Curt. in South Africa. They found that an epizootic caused by this fungus resulted in a reduction in the insect parasites and predators as well as the host and thus, when conditions became unfavourable for the fungus, the host was able to increase above its normal level. There is some danger that this might occur with other insect pests.

Thus it is evident that the utilization of parasitic fungi has its advantages and disadvantages and that considerably more fundamental research is necessary before the method can be applied to best advantage. Some progress has and is being made but too much should not be expected as long as the gross neglect and lack of understanding continues. The limitations to this method of control should not close our minds to its possibilities.

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### DISCUSSION

F. G. HOLDAWAY. The fungus *Beauveria bassiana* has been reported by Dr. Ralph Bird of Manitoba on adults of sweet clover weevil, *Sitona cylindricollis*. Ellingbow, Kernkamp, Haws and Christianson at the University of Minnesota have recently demonstrated that *B. bassiana* is capable of killing both adults and larvae of the sweet clover weevil. In view of the fact that the larvae live in the soil and larvae life extends over many months, one would expect that the microclimate of the soil would be important as a factor in infection of the larvae. I would like to know if anyone has any information that might have a bearing on this problem of infection by this fungus in the soil.

D. M. MACLEOD. Strains of *B. bassiana* have also been isolated from the sweet clover weevil in Canada. I have no specific data regarding the importance of microclimate in successful attempts to control insects with *B. bassiana*. I do think, however, it is extremely important and may explain why this fungus seems to be more important in controlling hibernating insects after they enter the ground, rather than in their feeding stage.

H. BLUNCK. How do you explain the curious situation that now we have much better results with fungous diseases in biological control of pests than in former times? I remember the experiments with *Empusa* against the grasshoppers in South America and in the northern parts of Africa. In the beginning there was complete success and then no more. It was believed that there must be special conditions in the insects themselves and in climate conditions. Is that not true?

R. B. BAIRD. Although the earlier workers on locusts claimed to have obtained success with *Empusa grylli*, it is now felt that they were, in effect, distributing some other fungus and the resulting control was caused by naturally-occurring fungi. Fungi do require special conditions but the actual requirements, be they climatic or otherwise, are poorly understood.

E. A. STEINHAUS. Microclimates are very important in fungus control. This is currently seen in alfalfa fields in California where *Empusa* has been important in suppressing populations of the aphid.



# The Use of Certain Entomogenous Microorganisms to Control the Alfalfa Caterpillar

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## ABSTRACT<sup>1</sup>

*Field tests have been conducted comparing application of a polyhedrosis virus and bacillus thuringiensis as control measures for the alfalfa caterpillar, Colias philodice eurytheme Bdv. In addition, combinations of the two agents were tested to determine if the shorter incubation period of the bacillus and the higher insect mortality rate of the virus could be obtained in one application. Bacteria-virus combinations produce the advantage of a short incubation period and quick mortality of the bacterial disease followed by more complete mortality due to the virus. While insect mortality was more quickly obtained by this method, the control obtained was not as complete or long lasting as that obtained by application of the virus alone. The use of the bacillus alone was more effective only in those cases in which field populations of the caterpillar were too near maturity for satisfactory control by the virus.*

The complete text has been submitted to the *Journal of Economic Entomology*.





# General Summary and Review of Utilization of Disease to Control Insects<sup>1</sup>

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## ABSTRACT

*Disease organisms may be utilized to control insect pests in two principal ways: as insecticides for the immediate destruction of insect populations; and as parasites to reduce the host population to a lower level. Various requirements of both the hosts and the disease organisms must be fulfilled if disease is to be successfully utilized in either of these ways. Therefore, though the dissemination of diseases by man has controlled a few specific insects, many other attempts have failed and there are definite limitations to the method. Some limitations are imposed by the biology and habits of the host insects, others by the characteristics of one or more groups of disease organisms, and others are common to disease organisms in general. Among the latter limitations are the high cost of production of micro-organisms, their lack of active mechanisms for dispersal, their susceptibility to climatic factors, their low pathogenicity, and the great variation in susceptibility to infection displayed by individual host insects.*

Under natural conditions outbreaks of insects are frequently terminated by diseases and insects continually suffer from a variety of diseases that form an important part of the mortality factors acting against their populations. Many attempts have been made to utilize diseases for the control of insect pests. The successful manipulation of a disease must result in economic benefits greater than the cost of treatment. Some attempts to control insects by the distribution of disease organisms have been failures. Others have been successful in producing some mortality of the insect population, but failed to reduce the population and the damage to a level commensurate with their cost. There are several successes of the method, some of which have been discussed in this symposium. At this stage in our attempts to use disease for control, it is advisable to consider some of the reasons for success or failure and to speculate on the future of the method and the conditions favourable for success. There is no vast body of factual information on the reasons for success and failure of attempts to control insects by disease, as studies of the failures have usually been dropped before the causes were elucidated and the number of successes has been too few to allow the deduction of generalizations. We may examine the future of the method and the types of problems, hosts, and organisms with which successful control may be obtained by considering its limitations.

Limitations to the successful utilization of diseases for insect control are imposed by the biology and characteristics of both the host insects and the disease organisms. Some hosts do not lend themselves readily to control, e.g. those with tunneling habits and those with sucking mouth parts. Disease is a density-dependent factor of mortality, i.e. it affects a greater proportion of the population as the density of the population increases. Thus insects that live in aggregations or that form large populations are more susceptible to epizootics than are those at low population densities. When the host density at which a disease is effective is higher than can be tolerated economically, utilization of the disease will not give economic control.

Each group of disease organisms has some characteristics that limit its utilization in control. For example, the fungi normally require moist conditions for both the production and the germination of their spores; many bacteria are susceptible to desiccation and insolation, attributes that limit their utilization in dusts and sprays; the protozoa often attack specific tissues of secondary importance to the host and may produce infections that are non-lethal or slow to kill; and most of the viruses are confined to hosts of the order Lepidoptera.

Other limitations are more or less common to the method in general and include the cost of production of micro-organisms, their lack of active mechanisms for dispersal,

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<sup>2</sup>Entomologist.

their disappearance from the micro-habitat of the host, their pathogenicity, and the great variation in susceptibility to infection displayed by individual host insects.

Problems of producing and storing pathogenic organisms in quantities sufficient for field application may restrict the use of the method.

The effectiveness of disease organisms is limited by their lack of active mechanisms for dispersal and transmission. Passive transmission is responsible for the fact that diseases are density-dependent. The fungi are best equipped to secure their own transmission by means of externally-borne spores, but among the other groups of micro-organisms the infectious agents may be trapped within the bodies of their hosts until liberated by decomposition of the host after death. Except where the main site of the infection is the alimentary canal, the living, infected host is not a potent source of infection for its fellows. During the interval between death of the host and liberation of the pathogens, potential sources of reinfection may be lost.

Lack of persistence in the microhabitat of the host may limit the use of a micro-organism for control. Disease organisms lose their viability to varying degrees when exposed to desiccation or insolation, and, under the washing action of wind and rain, even resistant stages tend to disappear from exposed surfaces where feeding insects may encounter them. Thus, large doses applied for control may be diluted to ineffective concentrations. The ability of an organism to persist at infective doses from one generation of the host to another, particularly in univoltine hosts, is of prime importance in determining its effectiveness as a continuing factor of mortality. The fungi and bacteria apparently persist in the soil from one year to another. Reinfection of the host population the following year begins by the chance infection of a few individuals with dusts containing the disease organisms, and thus the disease may appear too late to exert control. Viruses and microsporidia that can be transmitted from one generation to another by the egg are more likely to be continuously important mortality factors.

The length of the period between infection and cessation of feeding or death may influence the degree of control. In most insect diseases, the host dies shortly after it ceases to feed. A long period between infection and death increases the damage done by the insect and delays the transmission of the disease. The microsporidia and viruses require longer periods to complete their development and kill the host than do the bacteria or fungi, and must be applied to the early stages of the host in order to prevent excessive damage.

The most important factors that limit the effectiveness of diseases in control are the pathogenicity of the disease organisms and the resistance of the host insects to infection. It is not possible to separate these two factors but we can measure their interaction by the dose required to initiate infection. Insect populations respond to increased doses of pathogenic organisms by increased infection so that dosage-infection or dosage-mortality curves can be drawn. These have a sigmoid shape, and, like the dosage-response curves for insecticides, can be converted into straight lines by plotting the logarithm of the dose against the mortality in probits. Each pathogenic organism has a characteristic log-probit curve for its action on a given population of its host insect, and the median infective dose or median lethal dose (the LD.50) is the best numerical measure of the pathogenicity of the organism for a given host. Median lethal doses of different diseases vary widely in magnitude. For example, the LD.50 of *Bacillus larvae* White, ingested by young honeybees, is about 35 bacterial spores per larva; the LD.50 of the virus of *Bombyx mori* L. is about one million polyhedral bodies per silkworm larva (Bergold, 1953) and the LD.50 of the virus of *Porthetria dispar* (L.) is about 5.5 million polyhedral bodies per gypsy moth larva (Bergold, 1953).

Thus an insect population must be exposed to a substantial dose of pathogenic organisms for half of it to become infected. When the required doses are very great, the use of the disease for control may be economically impractical. One would expect greater success from the artificial distribution of a pathogen with a low LD.50 than of one less virulent. Thus the high pathogenicity of the virus of *Neodiprion sertifer* (Geoff.) is a prime factor in its use to control the European pine sawfly; the LD.50 is 100-500 polyhedra per larva per os (Bird and Whalen, 1953). On the other hand, the Japanese beetle is controlled by organisms of lower virulence; the LD.50 is about

two million spores of *Bacillus popilliae* Dutky per gram of soil; the actual ingested dose is unknown (Beard, 1944).

The LD.50 of a pathogen for a host may fluctuate rather widely because strains of the pathogen vary in virulence and host populations display variable resistance. Insect populations may have different degrees of resistance to infection at different ages or under different conditions of stress.

The median lethal dose only partly describes the reaction of an insect population to infection by a pathogen. The other significant feature of a log-probit curve is its slope. Curves for insect diseases are characterized by extremely low slopes when compared with curves for insecticides, as shown in Figures 1 and 2 where data on several insect diseases have been plotted to the same scale.

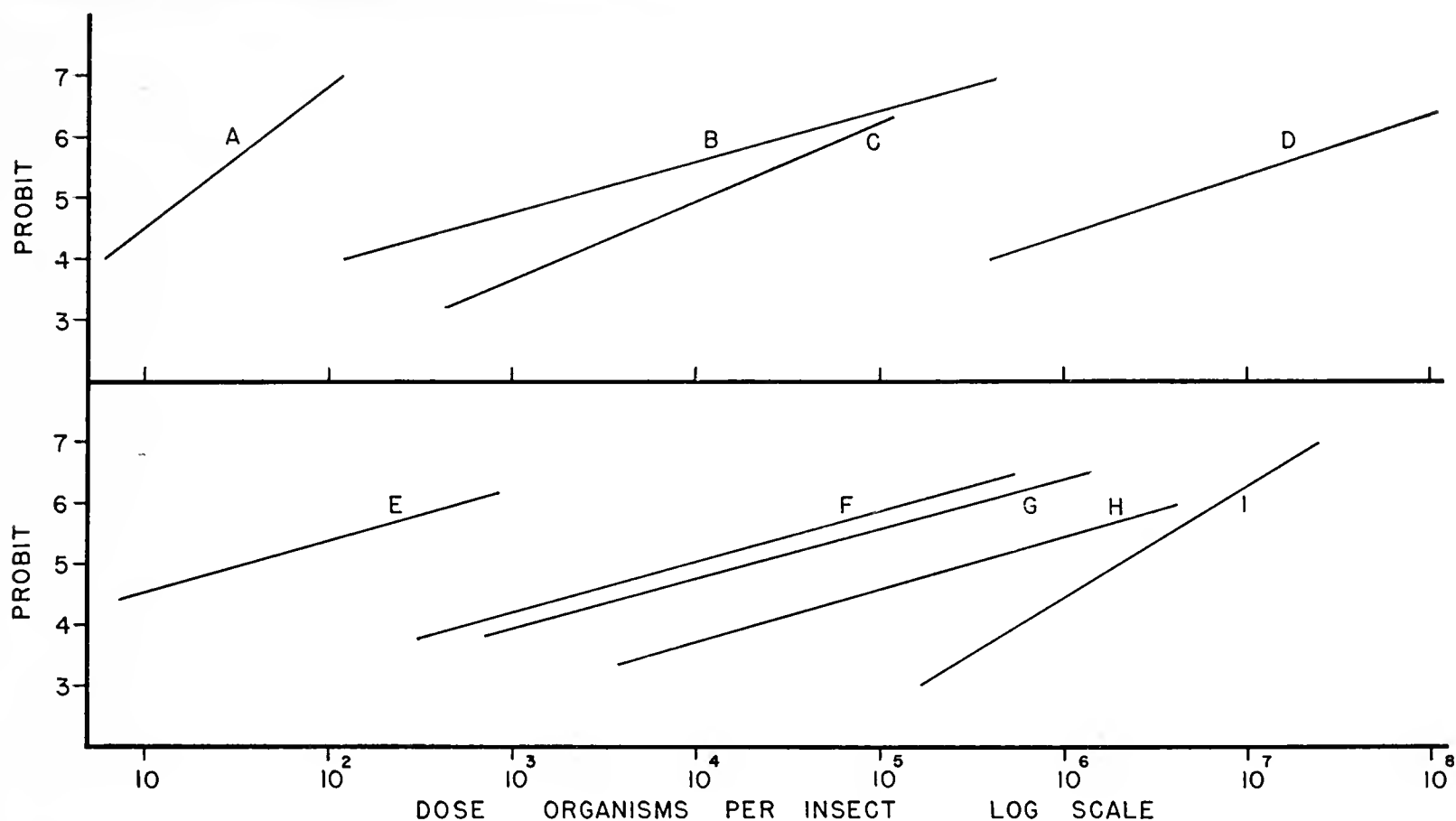


Fig. 1. Dosage-mortality curves of the action of insect pathogens acting on their normal hosts. In Curves A-D, the pathogens were placed in direct contact with the susceptible tissue by inoculation into the haemocoel. A. The bacterium, *Pseudomonas aeruginosa* (Schroeter) Migula, on adult grasshoppers, *Melanoplus bivittatus* (Say); (Bucher and Stephens, in press). B. The virus of *Bombyx mori* L. on larvae of the silkworm; data (Bergold, 1947) converted from grams of purified virus protein to estimated number of virus particles on the basis of particle weight (Bergold, 1953). C. The bacterium, *Bacillus popilliae* Dutky, on larvae of the Japanese beetle, *Popillia japonica* Newm.; (Beard, 1944). D. The polyhedral virus of *Choristoneura fumiferana* (Clem.) on larvae of the spruce budworm; data (Bergold, 1951) converted from grams of purified virus to estimated number of virus particles. In Curves E-I, the pathogens were ingested with the food. E. The bacterium, *Bacillus larvae* White, on very young larvae of the honeybee, *Apis mellifera* L.; (Woodrow, 1942). F. The microsporidian, *Nosema locustae* Canning, on adult grasshoppers, *Melanoplus bivittatus*; (Bucher, unpub.). G. The bacterium, *Pseudomonas aeruginosa*, on adult grasshoppers (Bucher and Stephens, in press). H. The virus of *Malacosoma disstria* Hbn. on larvae of the forest tent caterpillar (Bucher, unpub.). I. The bacterium, *Bacillus popilliae*, on larvae of the Japanese beetle (Beard, 1944); dose expressed as the number of spores per gram of soil containing the host larvae.

In Fig. 1, the upper group of curves, A to D, illustrates the mortality response of several insect populations to pathogens inoculated into the haemocoel, and the lower group, E to I, the response to pathogens ingested with the food. The characteristic feature of all these curves is their low slope irrespective of the absolute value of the LD.50, the taxonomic position of the pathogen and the host, or the method of infection.

In Fig. 2, the upper group of curves, J to L, shows the response to bacterial pathogens whose virulence is attributed to the toxic action of crystals formed within the sporangium at sporulation. Though the dose is measured in spores per insect, the spores were mixed with a considerable but unknown quantity of the toxic crystals. All three curves have slopes significantly higher than those for other diseases. The lower group of curves, M to R, shows the response to a variety of insecticides when the dose

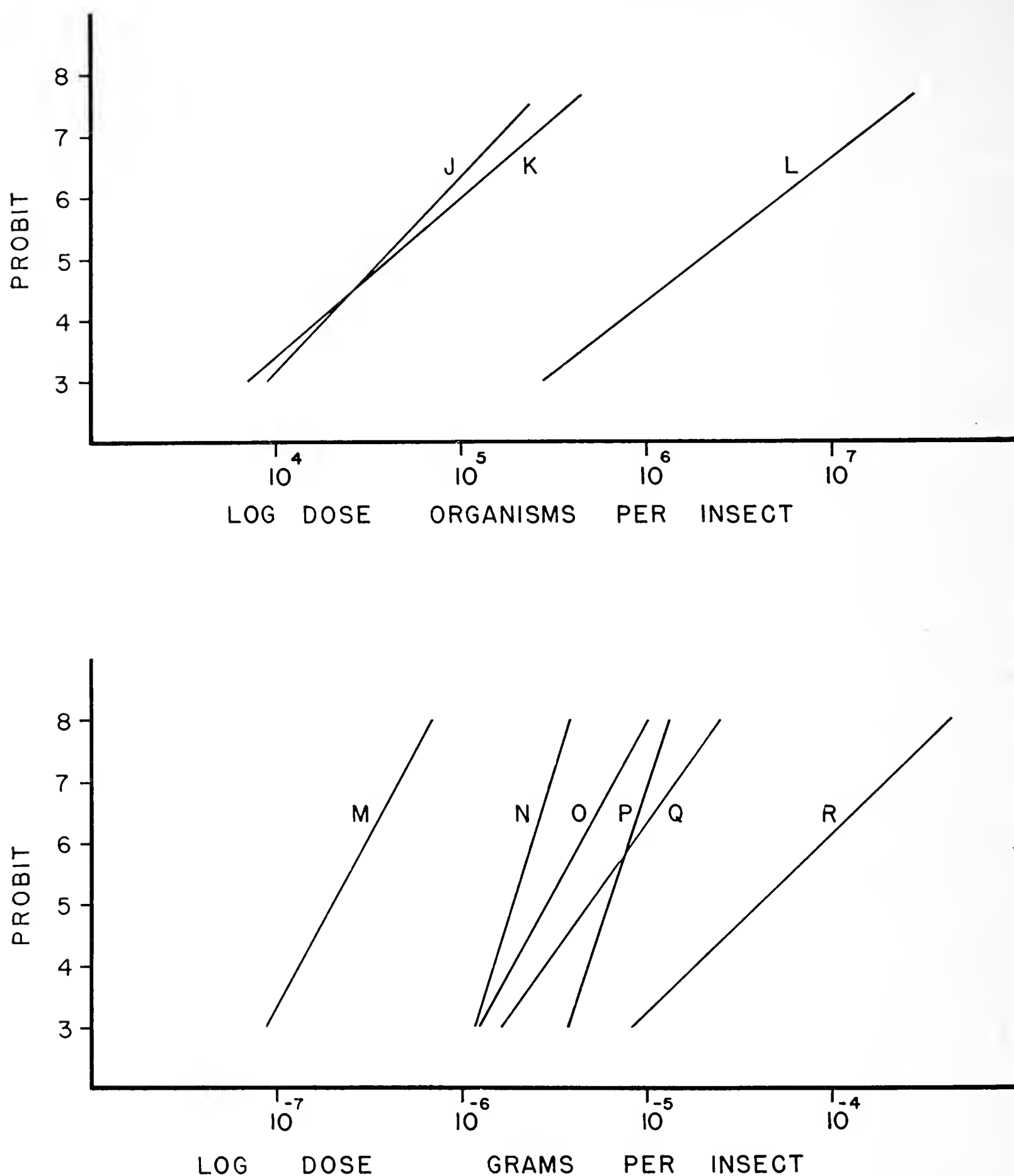


Fig. 2. Dosage-mortality curves of the action of insecticides and of bacterial pathogens whose virulence is attributed to the toxic action of parasporal crystals. In Curves J-L, the dose is expressed as the number of spores ingested per insect but contains a considerable though unknown quantity of parasporal crystals. J. The bacterium, *Bacillus sotto* Ishiwata, on larvae of the silkworm (Angus, 1956a). K. The bacterium, *Bacillus thuringiensis* Berliner, on larvae of the imported cabbageworm, *Pieris rapae* (L.); (Tanada, 1953). L. The bacterium, *Bacillus thuringiensis*, on larvae of the silkworm (Angus, 1956a). In Curves M-R, the insecticide was applied to the insects in various ways. M. Purified parasporal crystals of *Bacillus sotto*, fed to larvae of the silkworm; dose in grams per larva (Angus, 1956b). N. Solution of nicotine alkaloid injected into the pharynx of larvae of the silkworm; dose in grams per gram of insect (Hansberry, etc. 1940). O. Solution of DDT in benzene applied topically to the thorax of adult house flies, *Musca vicina* Macq., of normal resistance; dose in grams per fly (Tahori, 1955). P. Arsenic trioxide injected into the haemocoel of adult female cockroaches, *Periplaneta americana* (L.); dose in grams per gram of insect (Forgash, 1956). Q. Rotenone sprayed on the chrysothanthemum aphid, *Macrosiphoniella sanborni* (Gill.); dose in grams per litre of spray (Finney, 1952). R. Solution of DDT in benzene applied topically to the thorax of adult house flies of high resistance; dose in grams per fly (Tahori, 1955).

is expressed in grams of insecticide and plotted to the same scale as the curves for insect pathogens. The slopes of the dosage-mortality curves of insecticides are all significantly greater than those of insect disease organisms. The curve (M) for the



purified parasporal crystals of *Bacillus sotto* Ishiwata, has a steep slope similar to those for the insecticides. It is of interest to note that the curve (R) of the response of resistant house flies to DDT has a slope much lower than that of normal house flies (O) to the same insecticide.

The slopes of all curves are expressed as the change in the value of the ordinate in probits that occurs in response to a tenfold increase in the dose. The values for the slopes and the LD.50s are assembled in Table I.

TABLE I — The LD.50 and slope of dosage-mortality curves of insect disease organisms compared with those of insecticides. The dose is expressed as number of organisms per insect or the number of grams of insecticide per insect. The slope is expressed as the change in the value of the ordinate in probits that occurs in response to a tenfold increase in the dose.

	LD.50	Slope
A. <i>Pseudomonas aeruginosa</i>	17	2.34
B. <i>Virus Bombyx mori</i>	2,000	0.82
C. <i>Bacillus popilliae</i>	11,000	1.35
D. <i>Virus Choristoneura fumiferana</i>	4,000,000	0.93
E. <i>Bacillus larvae</i>	35	0.82
F. <i>Nosema locustae</i>	9,000	0.84
G. <i>Pseudomonas aeruginosa</i>	19,000	0.83
H. <i>Virus Malacosoma disstria</i>	300,000	0.86
I. <i>Bacillus popilliae</i>	2,000,000	1.83
J. <i>Bacillus sotto</i>	38,000	3.10
K. <i>Bacillus thuringiensis</i>	41,000	2.58
L. <i>Bacillus thuringiensis</i>	2,000,000	2.25
M. <i>Bacillus sotto</i> crystals	$2.0 \times 10^{-7}$	5.5
N. Nicotine alkaloid	$1.9 \times 10^{-6}$	9.6
O. DDT	$2.9 \times 10^{-6}$	5.5
P. Arsenic trioxide	$6.2 \times 10^{-6}$	9.1
Q. Rotenone	$5.8 \times 10^{-6}$	5.0
R. DDT	$4.0 \times 10^{-5}$	2.9

The slope of a dosage-mortality curve is a measure of the variation in resistance displayed by individual members of the population to the treatment; the lower the slope the greater the variability between individuals. Insect populations display intensely greater variability in their resistance to infection by disease than to the toxic action of insecticides. For example, if a population of insects is exposed to 10 times the LD.50 of an insecticide, all will die. An exception is the case of DDT-resistant flies where 10 times the LD.50 raises the probit to 7.9 and the mortality to 99.8 per cent. However, with insect diseases a tenfold increase in the dose has much less effect. For example, if grasshoppers are fed 10 times the LD.50 of *P. aeruginosa* (Curve G), the probit is raised from five to 5.83 and the mortality from 50 per cent to about 80 per cent; to raise the mortality to 99 per cent, a dose about 1,000 times the LD.50 would be required. The same is true for the other diseases. The Japanese beetle shows less variability of response; to raise the mortality from milky disease to 99 per cent requires a dose about 20 times the LD.50 (Curve I).

The fact that insects display great individual variation in susceptibility to infection by disease organisms has an important bearing on the utilization of diseases for insect control. It has good as well as bad features. The bad features are evident. Some insects in the population will not develop infection even when exposed to massive doses. Therefore, the control exerted by the disease may be at a level above that at which economic loss occurs. On the other hand, some individuals in the population are highly susceptible to infection at doses many times lower than the LD.50, and these may serve as foci of infection and aid the disease to persist.

Disease organisms may be used to control insect pests in two principal ways. They may be used in the manner of insecticides where the chief end in view is the immediate destruction of an insect population to protect a crop from damage. The use

of virus to control the alfalfa caterpillar in California is an example. Or they may be used, much as insect parasites and predators are used, where the chief end in view is the introduction of biotic mortality factors that will reduce an insect population to a lower, sub-economic level. Though there is some overlapping of purpose and effects, most of the attempts to control insects by disease can be assigned to one or other of these general fields of application.

Successful control of an insect by disease demands certain characteristics of both the host and the pathogen, and while these are common to both methods of use, they may assume a different relative importance depending on whether the pathogen is being used as an insecticide or as a parasite.

When diseases are used as insecticides the members of the insect population must be reached by an infective dose of the pathogen; the host or its food must be exposed to the artificial application of the pathogenic agent. The principal characteristics of a desirable pathogen are high virulence, ease and cheapness of production and application, speed of action, maintenance of viability, and some degree of persistence and infectivity over a range of climatic conditions. Transmissibility and persistence from one generation to another are of lesser importance because control demands high mortality and rapid protection and therefore implies that the whole population has been exposed to an infective dose and that repetitive treatment will be applied when necessary to protect a high value crop. When applied as an insecticide, the disease must compete with insecticides on the basis of induced mortality, availability and ease of application and cost. As shown above, most insect diseases do not compete with insecticides on the basis of the dosage-mortality response elicited in insect populations and it is frequently impractical to apply doses of pathogens large enough to infect 95-99 per cent of the population. Most of the attempts to control insects by diseases might be classified as attempts to use micro-organisms as insecticides and many of these have failed for the above reason. The successful use of diseases as insecticides in the future will depend on the discovery of organisms of high virulence. Disease disturbs the other biotic factors to a lesser extent than do insecticides; insects may be less likely to form disease-resistant than insecticide-resistant strains; and the use of disease organisms avoids the problems associated with the toxic residues of insecticides. The future may produce examples of successful control by diseases applied as insecticides by virtue of these secondary benefits.

When diseases are used as parasites, the principles are analogous to those used in the introduction and establishment of insect parasites or predators, and the success of the method may be judged by the same criteria. The characteristic feature is the introduction of the disease into a locality in which it does not already exist. The introduction may be a local or a regional distribution or redistribution or it may involve the importation of the disease from another country or continent. Successful examples of the method are the control of the Japanese beetle in the United States and of the spruce and pine sawflies in Canada, cases in which the host itself was originally introduced. Future successes may be expected where an insect pest has invaded a new region without its native diseases, although there is some hope that diseases can be introduced for the control of native insects.

The primary requirement is the persistence of the pathogen as a biotic factor of control of the host population. The pathogen must maintain itself at infective doses in the microhabitat of the host during the infective period and from generation to generation. In the sawfly diseases this is accomplished by transmission of the viruses by the eggs and the development of disease in very young larvae that serve as foci of infection for the new population. In the Japanese beetle disease, the infective spores persist in a viable state and accumulate in huge numbers in the soil in which the grubs live. Other desirable attributes are high virulence, ease of transmission, independence of climatic conditions, maintenance of viability, resistance to unfavourable factors of the host's environment, and ease of dissemination without human intervention. The Japanese beetle disease spreads slowly and a program of mass distribution was instituted to remedy this. Other attributes such as cost and the ease of production and application may be only of secondary importance, because the successful use of diseases as parasites implies a high degree of permanence without the necessity of

continuous re-application. The speed of action and of control may be of minor importance as the method must be judged on its long-term benefits rather than on its immediate effects.

It should not be expected that all introductions of diseases will produce the same degree of control as the diseases of the Japanese beetle and the sawflies. The establishment of a disease on an insect population may result in a much smaller population decrease and still be an important addition to the biotic factors of control. Thus the future use of diseases as parasites is likely to be successful in fields where other biological control agents might be expected to be successful, i.e. on crops where some damage can be tolerated economically.

In the past, many attempts to use diseases for control have failed because the investigators applied diseases without consideration of the principles and limitations of their use, or without any distinction in the manner of application or in the purpose for which they were applied. In the future we may expect more careful basic investigations and a more careful selection of both the host and the pathogen with which control will be attempted, and thus a larger proportion of successful cases of control. The use of diseases for control is not applicable to all insects, the method has a number of limitations, but we may expect it to be a tool of increasing importance in our fight against insect pests.

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### DISCUSSION

J. FRANZ. The method of comparing variation in susceptibility of insects to insect pathogens by the use of slopes of dosage probits is, no doubt, very helpful. I should be glad, however, to see the probit curves of such pathogens which showed the greatest practical success in field application, like viruses of sawflies and of *Colias eurytheme*.

C. G. THOMPSON. The minimum dosage required for near 100 per cent infection of alfalfa caterpillar populations is one billion polyhedra per acre.

E. A. STEINHAUS. From a pragmatic viewpoint we should keep in mind that even large doses of an infectious agent may be entirely practical, easy to apply, and avoid the toxicity of insecticides.

G. H. BERGOLD. In case of the low-virulent lepidopterous viruses, we probably have a similar situation as in the milky disease of the Japanese beetle: In the field the virus has to build up to enormous concentrations before it will control an outbreak of insects.

T. A. GOCHNAUER. The data on LD.50 levels of *Bacillus larvae* for honeybee larvae ignore differences between strains in host susceptibility and pathogen virulence. Where were the data obtained?

G. E. BUCHER. Data were obtained from Woodrow.



# Is There a Possibility of Using Microsporidia for Biological Control of Pieridae?

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## ABSTRACT

In reviewing the Microsporidia of Pieridae, we have found that more than half a dozen species are detected to date, but only four are distinctly characterized. They attack *Pieris brassicae* L., *P. rapae* L., *Aporia crataegi* L. and perhaps also other species of Pieridae. Some species parasitize only one organ (fat cells respectively midgut), others (*Perezia legeri* Paill.) two or three (fat tissues and certain giant cells of the blood) and the rest (*Perezia mesnili* Paill., *P. mesnili* sensu Tanada, *Nosema polyvora* Blunck) nearly all tissues. Several species, perhaps most of them, cause infection by way of the digestive tract of the host (*Perezia mesnili* Paill., *P. mesnili* sensu Tan., *N. polyvora* Bl., *Plistophora prope schubergi* Zw.); others are transovarially transmitted, for example *Pieris mesnili* Tan., *Perezia legeri* Paill. only infect *Pieris brassicae*, if the caterpillar already is parasitized by *Apanteles glomeratus* L. In the midgut of the wasp this Microsporidia often multiplies. *N. polyvora* Bl. and perhaps *Thelohania mesnili* Paill. also are able to propagate in this braconid. Transmission into the larva, resp. into the caterpillar in these cases may occur by direct infection of the embryo of the wasp or by contaminating the surface of the egg with spores, when it is laid. In *Pieris mesnili* this has already been proved by Tanada. There are also microsporidians in the parasites of *A. glomeratus* L., for example in the ichneumonids, *Haplaspis nanus* Grav., *Hemiteles simillimus sulcatus* Bl. and *Thysiotorus brevis* Thoms., in the Chalcidoidea, *Tetrastrichus rapo* Walk. and *Dibrachys cavus* Walk., but most of them seem to be specific for these Hymenoptera. The European microsporidians for the Pieridae are comparatively harmless. Even if heavily infected, some caterpillars may be able to complete the metamorphosis. Sometimes when they are infected by *N. polyvora*, the females produce full-grown eggs. More fatal is *Pieris mesnili* Tan. to its host. For biological control of noxious Pieridae, European Microsporidia probably are not quite suitable.

Dr. J. Weiser has given us a complete survey on the Microsporidia living in insects. My paper deals only with the Microsporidia in Pieridae. These belong to the most numerous parasites. In spite of that they remained unknown until 1918. Paillot discovered the first species, which he described as *Perezia mesnili*. He reported it to be pathogenic for *Pieris brassicae* L. (1918). A short time later he described three other species. In the laboratory Steinhaus and Hughes in 1949 succeeded in infecting *Pieris rapae* L. with their *Nosema destructor*, and in 1952 Hall, experimenting with the same insect, succeeded with his *Nosema infesta*. Recently we found Microsporidia in *Pieris brassicae*, *P. rapae*, *Aporia crataegi* L., their parasites and hyperparasites.

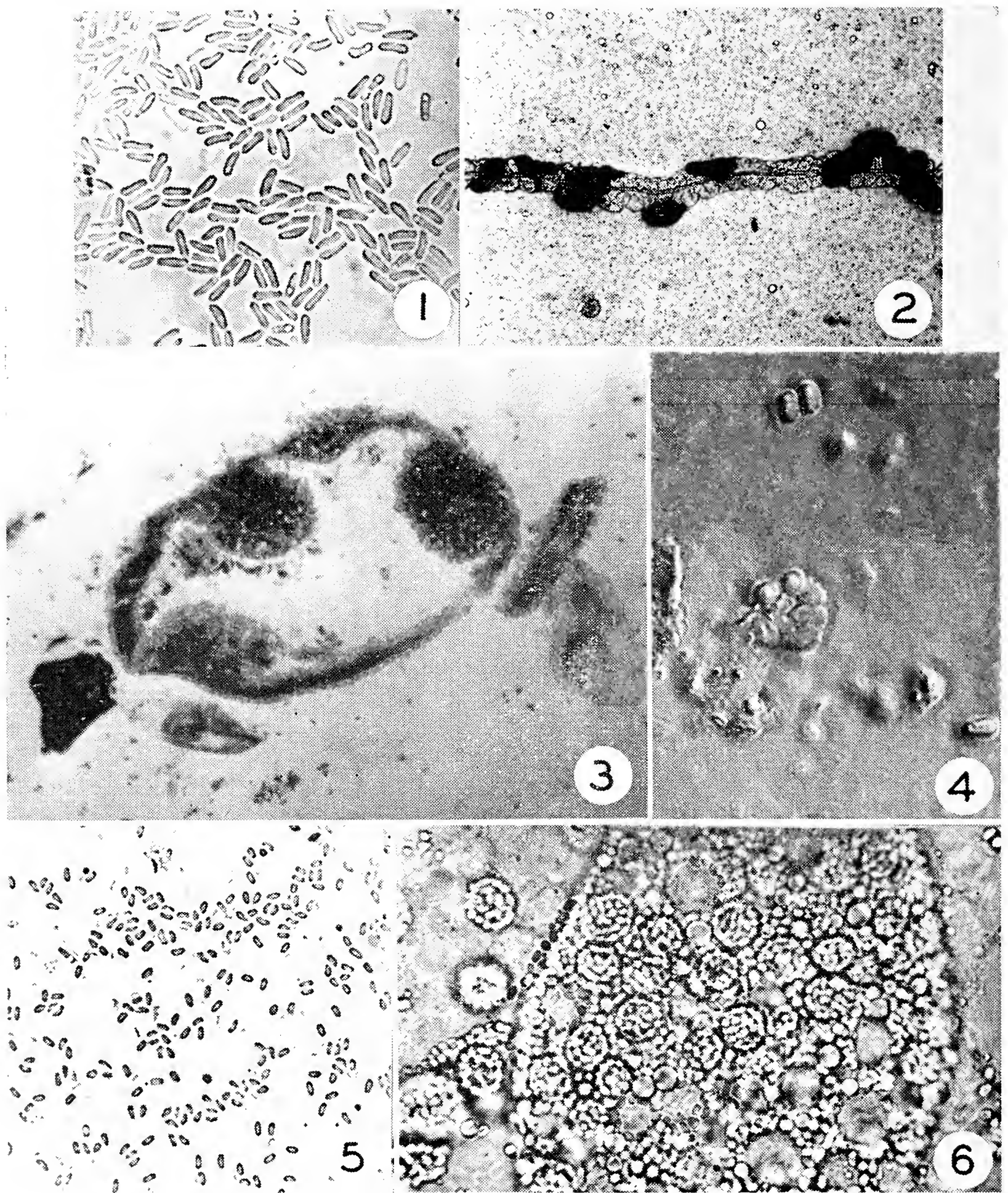
We paid particular attention to the question of the pathogenic importance of these protozoans and of the possibility of using them for biological control. This point of view seemed to be justified, because other Microsporidia act as morbidic agents, e.g. in *Bombyx mori* L., *Apis mellifica* L., *Euproctis chrysorrhoea* L., *Lymantria dispar* L., *Malacosoma neustria* L., *Hyphantria cunea* Drury and *Hyponomeuta malinellus* Zell. (Zwölfer, 1927a; 1927b, Weiser and Weber, 1956). Paillot (1928) estimates the role, Microsporidia play in gradation ("Massenwechsel") of insects more important than that of the bacteria. To date Weiser has even explained, that according to his experience, most of the Microsporidia living in insects are fatal for their hosts.

The first species and also the most frequent, we found in our collection, was *Nosema polyvora* Bl., on which I reported at the Amsterdam Congress in 1952. It is possible that *N. polyvora* is the same kind, which Paillot called *Perezia mesnili*. This may be a species, which has spread over the whole world, because Tanada (1953, 1955, 1956), found it even in Hawaii. We do not risk the identification up to this time, missing perhaps with some exceptions, the pansporoblasts of *Perezia*. Besides that there



are differences in the structure of the spores, in the behavior and in the pathogeny of these microsporidians.

The spore of *N. polyvora* is elongated and comparatively slim (Fig. 1, Table I). The polar filament, extruded after an addition of acetic acid (Fig. 7), appears to be 40-60 $\mu$  in length, the maximum length was 92 $\mu$ .



We found *N. polyvora* parasitizing several hosts of different kind, above all the caterpillars of *P. brassicae*, but it may as well infect the imported cabbageworm, *P. rapae*.

An artificial infection of the caterpillars of *A. crataegi* succeeded easily. We found this species multiplying also in *Apanteles glomeratus* L., the most important social parasite of the larvae of these Pieridae. It may be, that *N. polyvora* and — as we suppose — other Microsporidia as well, are developing in *Hemiteles* and *Gelis*, which belong to the most common hyperparasites of *P. brassicae* and *A. crataegi*.

As to the infected organs *N. polyvora* is just as unspecific as *Perezia mesnili*. Very often it is parasitizing the salivary glands and the midgut. In heavily attacked

TABLE I — Microsporidian Parasites of Pieridae.

Species	Host	Infected organ	Spore				Mode of infection
			Size in micron	Length by width	Quantity average in $\mu^3$	Length of the polar filament in micron	
<i>Nosema polyvora</i> Bl.	<i>Pieris brassicae</i> L. <i>Pieris rapae</i> L. <i>Aporia crataegi</i> L. <i>Apanteles glomeratus</i> L. etc.	mid-gut epithelium, salivary glands and nearly all other tissues	(3,3-5,0-5,7) x (1,5-1,9-2,5)	2,6:1	12,6	40-92	by oral ingestion, probably also by means of the contaminated ovipositor and through the eggs of <i>Apanteles glomeratus</i> L. or through the eggs of the butterfly
<i>Perezia mesnili</i> Paill.	<i>Pieris brassicae</i> L.	mid-gut epithelium, Malpighian tubes and nearly all other tissues	after Paillot: 3,4x(1,5-2) after Weiser: (4-5) x (1-2)	amply 2:1	?	? 18-20	by oral ingestion
<i>Perezia mesnili</i> Tan.	<i>Pieris brassicae</i> L. <i>Apanteles glomeratus</i> L.	mid-gut epithelium, Malpighian tubes and nearly all other tissues	(3,4-4,0-4,4) x (1,4-2,0-2,7)	2:1	?	33-54-88	1. by oral ingestion 2. through the eggs 3. by <i>Apanteles glomeratus</i> etc.
<i>Nosema</i> cf. <i>legeri</i> Paill.	<i>Pieris brassicae</i> L. <i>Apanteles glomeratus</i> L.	adipose tissue, "giant cells" of the blood	(3,3-5,0-7,7) x (2,0-2,2-3,7)	2,2:1	17,9	?	not by oral ingestion, perhaps by <i>Apanteles glomeratus</i> L.
<i>Perezia legeri</i> Paill.	<i>Pieris brassicae</i> L.	adipose tissue, "giant cells" of the blood, occasionally throughout the body	after Kudo: 4-5 after Weiser: (4-5) x (2-3)	? 2:1	?	30-40 (literature)	not by oral ingestion, perhaps transovarial or indirect by <i>Apanteles glomeratus</i> L.
<i>Perezia pieris</i> Paill.	<i>Pieris brassicae</i> L.	Malpighian tubes, salivary glands, intestinal tube	after Paillot: nearly the same as <i>P. mesnili</i> and <i>P. legeri</i>	2:1	?	?	by oral ingestion
<i>Thelohania mesnili</i> Paill.	<i>Pieris brassicae</i> L.	adipose tissue	(4,0-5,0-6,9) x (2,1-2,72-3,9)	1,84:1	27	?	by oral ingestion
<i>Plistophora</i> cf. <i>schubergi</i> Zwölfer	<i>Aporia crataegi</i> L. <i>Euproctis chrysorrhoea</i> L. <i>Pieris brassicae</i> L.	mid-gut epithelium	(1,8-2,4-3,4) x (0,9-1,34-1,7)	1,8:1	3	20-50	by oral ingestion

larvae in all kinds of tissues and organs spores may develop. The infected cells, especially those of glandular character, tend to become hypertrophic (Figs. 2, 3). These "giant cells" often contain some thousands of spores.

Most frequently the insects are infected by way of the digestive route. We easily succeeded in infecting caterpillars by feeding them with food containing spores. As we have already reviewed this elsewhere (Blunck, 1952) caterpillars of *P. brassicae* can also become infected, when they are living together with wasps of *A. glomeratus*. Perhaps the wasps transmit the spores mechanically, when they pierce the host putting in their eggs with an infected ovipositor. In one case we found spores in eggs of *Apanteles*. Further transmission of the microsporidia may occur transovarially by the butterflies of Pieridae, as almost all their internal organs can be infected. Maybe, the spores adhere on the outside of the eggs, maybe they are really internally infected. In the case of *Perezia mesnili*, Tanada (1955) has demonstrated that all these ways of infection are quite probable.

*N. polyvora* has comparatively low pathological efficacy to its host. It is a fact that young caterpillars which are extremely infected soon after birth show a reduced appetite, produce no fat, become dwarfed, and finally they die. Later infected caterpillars often achieve the metamorphosis. Slightly infected butterflies produce mature eggs. We conclude that the cytotoxic effect of the attack is unimportant. The death of strongly infected individuals is not caused by poison but by consumption of vital organs by the parasite.

A second microsporidian we observed less frequently. It may be identified with *Perezia legeri* Paill., but as we did not find pansporoblasts with certainty, this species may be designated today as *Nosema* cf. *P. legeri* Paill.

The spores are similar to those of *N. polyvora* but a little bit less slim. A vacuole is present at the thicker end of the spore, and well visible, if the spores are young enough. We did not succeed to effect an extrusion of the polar filament.

Surely *P. brassicae* is a real host to *N.* cf. *P. legeri* Paill. Probably however this microsporidian is developing as well in *A. glomeratus*, an opinion, regarding *P. legeri* has already been discussed, but denied by Paillot (1953). We frequently observed clusters of spores in the epithelium of the midgut, also in the so called "Schwanzblase", the spherical blister at the tail, in the silk glands of the larva and in the malpighian tubes of the adults (Table II).

TABLE II — Microsporidian Infections in *Apanteles glomeratus* L.

Number	State of the host of the Microsporidian	Infected organ	Number of measured spores	Size in micron	Ratio length by width	Quantity average in microns
1	larva	salivary glands	11	(3,5-3,8-4,3) x (2,4-2,5-2,5)	(1,5-1,5-1,7):1	16,75
2	"	"	20	(3,6-4,4-5,1) x (2,5-2,4-2,8)	(1,4-1,8-1,8):1	17,9
3	"	"	40	(4,9-5,0-5,8) x (1,6-1,9-1,9)	(3,1-2,6-3,1):1	12,7
4	"	epithel of midgut	22	(3,5-4,9-6,0) x (2,6-2,6-2,8)	(1,3-1,9-2,1):1	23,4
5	"	"Schwanz- blase"	14	(4,1-4,9-6,0) x (1,5-2,0-2,0)	(2,7-2,5-3,0):1	14,8
6	adult	malpighian tube	22	(5,5-6,9-8,0) x (2,5-2,9-3,4)	(2,3-2,4-2,4):1	41,0
7	"	"	20	(3,3-4,9-6,4) x (3,3-3,5-3,9)	(1,0-1,4-1,6):1	42,0



We do not mean to say, of course, that all these findings are necessarily true in the case of *Nosema* cf. *legeri* Paill., but at least partly so and especially in number 1 and 2 they are in keeping with the known measures of this microsporidian.

With regard to the infected tissues in *P. brassicae*, *N.* cf. *legeri* Paill. was observed to be much more specific than *N. polyvora* Bl. We found it only parasitizing the adipose tissue and certain "giant cells" being accompanied with infection of *A. glomeratus* L. After Paillot and later on after Kudo (1924) and Steinhaus (1949) in *P. legeri* Paill. occasionally a generalized infection occurs throughout the body.

The infection is not possible via the alimentary tract. All our experiments in this way failed. We suppose, however, that *N.* cf. *legeri* Paill. can be transmitted with the help of *A. glomeratus*, for an infection is always accompanied by presence of this braconid. We learned by experiments that probably the wasp actively transmits the spores by the same ways we described for *N. polyvora*.

The pathological effect of *N.* cf. *legeri* Paill. seems to be still smaller than that of *N. polyvora*. About all infected caterpillars matured for the metamorphosis, of course none passed to the next stage, because they all had been infected by *Apanteles glomeratus*.

In our experiments we did not realize the third species of *Perezia* described by Paillot (1924). That is *P. pieris* which was discovered near Lyon in France.

We found a fourth species of microsporidian belonging to the *Nosema-Perezia* group in one caterpillar of *A. crataegi*. The salivary glands were seriously attacked and its white sprinkling was visible with naked eye. Pansporoblasts were missing. One cell in the neutral epithelium around the nerve cord was also infected. At first we concluded that it was an infection of *N. polyvora*, but surprisingly all other organs had stayed without infection, even the midgut. Further, the size of the spores differed from *N. polyvora*. Twenty-six spores measured in an average  $4.8$  by  $2.6\mu$ , in the maximum  $6.0\mu$  in the length by  $3.0\mu$  in the width and in the minimum  $4.0\mu$  by  $2.6\mu$ . The ratio of length by width was  $1.8:1$ ;  $2:1$ ; and  $1.5:1$  respectively. The quantity averaged  $22.4\mu$ . That means, that the spores are thicker and have a larger quantity than those of *N. polyvora*.

To prove if these characteristics were constant or a consequence only of very favorable conditions of development, we started an artificial infection. We infected first and second instars of *A. crataegi* from outdoors by feeding them on plum leaves, contaminated with a fluid of the triturated salivary glands of the above mentioned third instar. Seventeen days later we dissected an infected third instar of our experiment, the silk-glands of which were infected. The spores even were enlarged, compared with those we had first found. They measured  $5-6\mu$  and more in length by  $2.4-2.8\mu$  in width. Perhaps not yet matured, they further seemed to be more conical at the vacuole bearing end. Pansporoblasts were missing again. With exception of the salivary glands no organ had become infected, neither the adipose tissue nor the midgut and the muscular system.

Our fifth species is *Thelohania mesnili*, the fourth microsporidian described by Paillot. It is quite different from all other species, but this microsporidian is so very rare in *P. brassicae* that we consider another insect being chief host to it. Paillot observed this species 1924 near Lyon. We found it later in three matured caterpillars of *Pieris brassicae*, which had developed on a cabbage field near Bonn and in 1955 in seven matured caterpillars of *P. brassicae* reared in our insectarium.

The spores are rather large and ovoid, rather more ovoid than those of our species of *Nosema*.

The most important stages of development are visible with contrast-phase microscope in the living object. The size of the globular or elliptical pansporoblasts (Fig. 4) containing 8 spores ranges from  $8.5\mu$  in diameter to  $12.4$  by  $9.0\mu$ .

Host to *Thelohania mesnili* Paill. is *P. brassicae* itself. Artificial infection of *P. rapae* and *A. crataegi* failed. It also failed in experiments with *P. brassicae*. Therefore it is uncertain whether or not this microsporidian is capable to developing in these two species of butterflies.

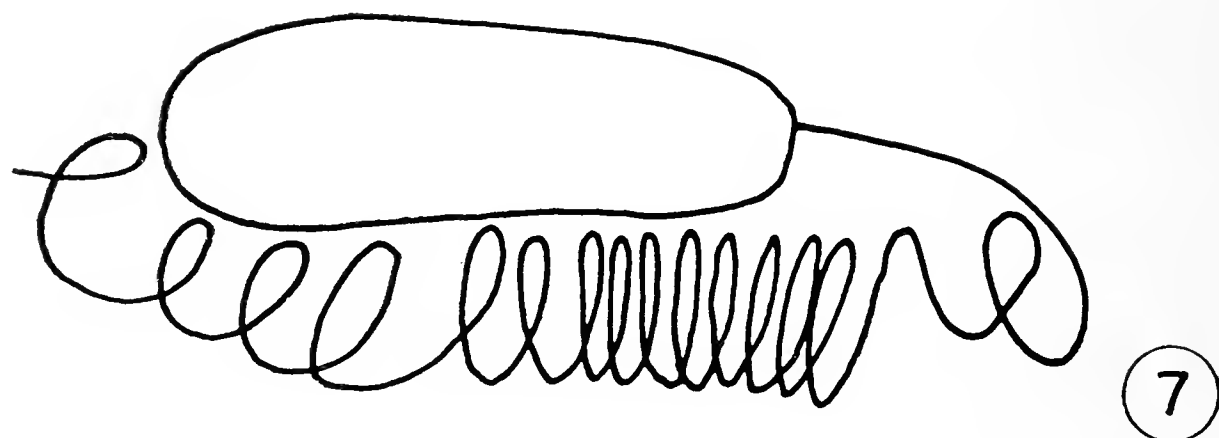
The principal infected organ is the adipose tissue. In this point we agree with Paillot (1933) and also in the observation that the occurrence of *T. mesnili* always is

accompanied by infection of the host with *Apanteles*. We observed only one exception, which is not yet perspicacious.

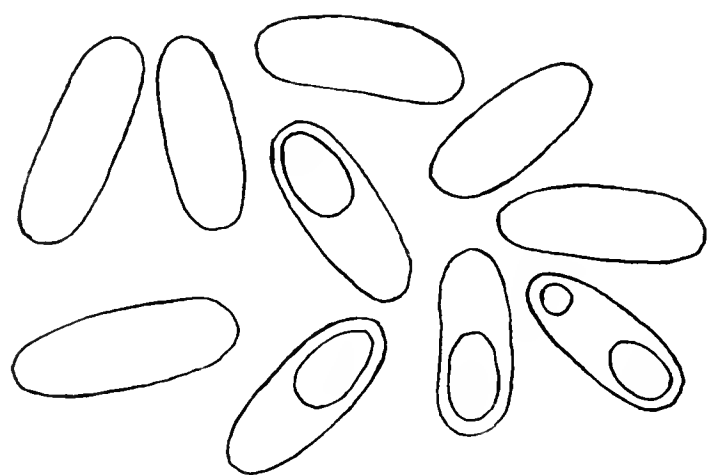
The transmission of spores seems to be dependent on *A. glomeratus*. So far it resembles that of *N. cf. legeri* Paill., but probably they are not capable of multiplying in the braconid. We observed the spores as well as the pansporoblasts—the last unmaturing and in the eight-cell stage—in the red-brown excrements of their larvae but never in any tissue, not even in the adipose tissue. Therefore we ask, should the spores pass a process of maturing in the gut of the braconid, thus becoming contagious, so that they may be capable of infecting a caterpillar after having been eaten by it?

The pathogenic effect of *T. mesnili* is small. The caterpillars pass to maturity and die only as they are attacked by *Apanteles*.

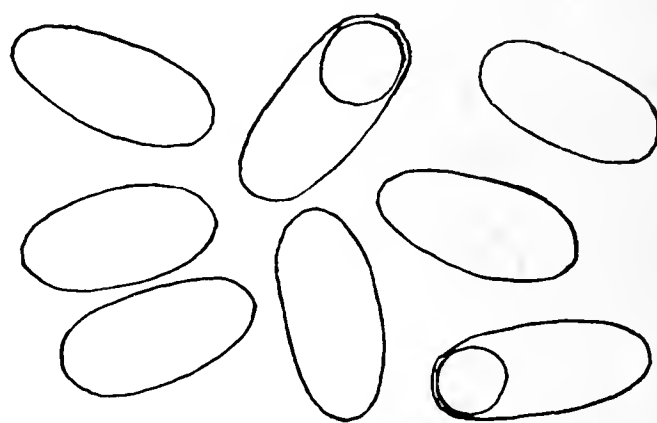
A sixth species, belonging to the genus *Plistophora*, we found in the caterpillars of *A. crataegi*, collected in April 1955 near Heidelberg and in some other places. This is apparently the first record of a *Plistophora* infection of Pieridae in the field. The parasite is morphologically and biologically similar to *Plistophora schubergi* Zw. (Zwölfer, 1927a; 1927b), but because of little differences, we prefer to name this species for the time being *P. cf. schubergi* Zw.



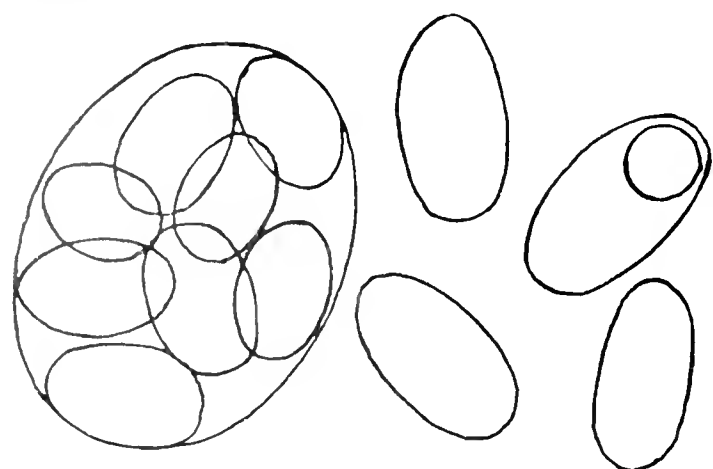
Nosema I



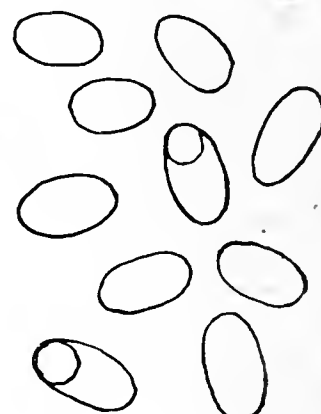
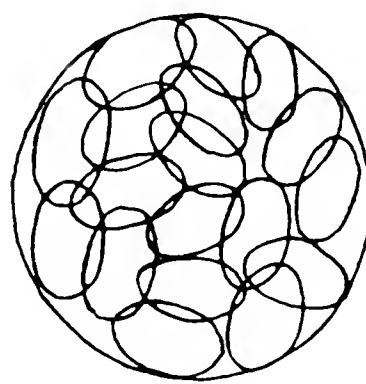
Nosema II



Thelohania



Plistophora



} 1  $\mu$



The spores (Figs. 5, 8) are ovoid and smaller than those of all other species parasitizing Pieridae. They are less light-reflecting and they become deformed more easily. The larger vacuole, present at the thicker end of the spore, is well visible in the contrast-phase microscope. In one case at the opposite end we observed the smaller one too. The polar filament was extruded after addition of acetic acid.

The life-cycle is unknown to date. The pansporoblasts (Fig. 6) are round and rather large. Matured they measure  $5\text{--}8\text{--}9\mu$  in diameter and often contained about 30 and sometimes about 60 spores. In slices, stained with Giemsa's stain, we often observed the schizonts, forming "chainettes", which occur in many species of microsporidia and in our *Nosema* too. These "chainettes" mostly are lying parallel to the longer-axis of the host cell, measuring 10, 20, 30 and even  $40\mu$  in length by  $3\text{--}4\mu$  in width, containing some circular spots faint in colour with about  $1\text{--}2\mu$  in diameter. Perhaps younger stages of this cycle might be presented by dumb-bell-formed parasites measuring  $4\text{--}6\text{--}8\mu$  in size. Stained with Giemsa, they are darker than the "chainettes" and contain as well nuclein faint in colour.

Our *Plistophora* was observed to infect only one organ, that is the epithelium of the midgut. Heavily infected excrements of *A. crataegi* become dirty yellow-brown instead of red. Infection occurs by way of the digestive route, we realized by experiment.

We suppose *A. crataegi* to be a real host of this species. Via the oral route we tried to infect also caterpillars of other Lepidoptera. Thus we intended to examine, if our microsporidian was identical with the true *P. schubergi*. The result shows that an artificial infection is easily transmitted not only from *A. crataegi* to *A. crataegi* (See Nr. 1) but also to *E. chrysorrhoea* (see Nr. 3). We were less successful in infecting *P. brassicae* (see Nr. 2). In one case only a caterpillar of *L. dispar* fell ill (see Nr. 4), and it is undecided whether or not the morbid agent came from the infective material we used. Spores gained from *P. brassicae* were contagious only in one case for a caterpillar of the same species (see Nr. 5). Experiments with *E. chrysorrhoea* and *L. dispar* failed (see Nr. 6, 7). Spores gained from diseased *E. chrysorrhoea*

TABLE III — Results of Infection Experiments with *Plistophora* cf. *schubergi* Zwölfer.

No.	Infection materials from	Experimental animal	Results			
			Positive		Negative	
			Number of experiments	Number of individuals	Number of experiments	Number of individuals
1	<i>Aporia crataegi</i> L.	<i>Aporia crataegi</i> L.	3	53	1	16
2	"	<i>Pieris brassicae</i> L.	4	21	2	84
3	"	<i>Euproctis chrysorrhoea</i> L.	2	11	1	13
4	"	<i>Lymantria dispar</i> L.	?1	?1	1	12
5	<i>Pieris brassicae</i> L.	<i>Pieris brassicae</i> L.	1	1	6	71
6	"	<i>Euproctis chrysorrhoea</i> L.	0	0	2	10*
7	"	<i>Lymantria dispar</i> L.	0	0	2	19
8	<i>Euproctis chrysorrhoea</i> L.	<i>Lymantria dispar</i> L.	0	0	2	22
9	"	<i>Pieris brassicae</i> L.	1	2	3	27
10	"	<i>Aporia crataegi</i> L.	1	1	0	1

\*In one of the untreated controls 1Lv was infected with *Plistophora* cf. *schubergi* Zwölfer

in two cases were contagious for *P. brassicae* (see Nr. 9), in one case for *A. crataegi* (Nr. 10) and in no case for *L. dispar*.

Our results with *Euproctis chrysorrhoea* agree to the question that our *Plistophora* sp. is similar to *P. schubergi*, which preferably infects these butterflies (Zwölfer, 1927a; 1927b). But as our parasite was not contagious for *L. dispar* the question of identity of these species can not be answered. That is impossible too because the spores of different origin differ in their pathogenic effect. All the hosts artificially infected with our spores from *A. crataegi* only became seriously ill, when the infection took place so heavily that the midgut of the caterpillars was fully destroyed, otherwise the caterpillars were able to develop into adults. An infected female of *Aporia crataegi* even produced many matured eggs. Zwölfer considers the infection produced by *P. schubergi* to be generally fatal to the host as well as to *E. chrysorrhoea* and *L. dispar*. He regards this microsporidian to have a great agricultural significance in controlling these two pests.

Finally we have to mention that there were some other cases of microsporidian attack in our material of Pieridae which we are unable to identify with the species here described. Among them are at least two species which do not live in the Pieridae themselves, but exclusively in the parasites and hyperparasites of these butterflies. Our knowledge, however, until now is too meagre to discuss these observations.

Recapitulating, we must conclude that until now there is little chance of using Microsporidia for biological control of injurious Pieridae.

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# Recent Advances in the Knowledge of Some Bacterial Pathogens of Insects<sup>1</sup>

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## ABSTRACT

Recent investigations in North America and Europe have focussed this work on the 'Bacillus cereus group' as pathogens of insects. A review of this work is presented.

It has been shown that the *B. cereus entomophytes* can be separated into two types. One type produces crystalline inclusions in sporulated cultures and a proteinaceous compound, toxic for insects, has been isolated from such cultures. The toxin appears to be associated with the crystalline inclusions. The other *B. cereus* type does not form crystalline inclusions but produces a toxic enzyme which breaks down tissue phospholipids.

Mode of action studies have shown that these toxic substances can cause death of certain insect species. The possibility of other factors contributing to virulence is discussed.

Laboratory and field feeding tests are reported and the implications of the histopathology, and interactions of the host and parasite, in these diseases are considered.

Some of the best known bacteria associated with insects are species of the genus *Bacillus*, and these include *B. cereus* Fr. and Fr., *B. thuringiensis* Berliner, *B. sotto* Ishiwata, and *B. cereus* var. *alesti* Toum. and Vago, all of which have been reported as pathogens of certain insects (Angus, 1956a; Heimpel, 1954; Steinhaus, 1951b; Toumanoff and Vago, 1951).

## NON-CRYSTAL FORMING STRAINS OF *B. CEREUS*

Since Steinhaus' review of the entomogenous bacteria in 1949, there have been many additional feeding tests made with a number of *B. cereus* varieties against several insect species. These tests and the results are summarized in Table I.

It will be noted that most of the tests are negative. Positive tests were obtained with certain strains only in the case of *Carpocapsa pomonella* (L.) and the sawfly species tested.

It has been suggested that the lecithinase (a phospholipase type C) produced by *B. cereus* var. *alesti* is, in part, responsible for the death of silkworm larvae, *Bombyx mori* L., infected by this bacterium. Toumanoff and his colleagues (Toumanoff *et al.* 1954) demonstrated that a lecithinase extracted after the method of Chu (1948) from *alesti* is toxic for silkworm larvae by injection, and that the resulting symptoms were those of natural bacillary flacherie.

Heimpel (1955b) showed that there was a correlation between the rate of lecithinase production by several *B. cereus* strains and their respective abilities to kill larch sawfly larvae. Species of the genus *Bacillus* that do not produce this enzyme are not pathogenic for the larch sawfly. Heimpel showed that 6.2% of a mouse LD<sub>50</sub> dose of lecithinase is the LD<sub>50</sub> by injection for the fifth-instar larva. The injected enzyme produced the same symptoms in the larvae that are encountered in insects infected with *B. cereus*.

Unpublished work by Kushner and Heimpel at the Forest Insect Laboratory, Sault Ste. Marie, has shown that phospholipids in larch sawfly larvae and in larvae of the forest tent caterpillar, *Malacosoma disstria* Hbn., are broken down, *in vitro*, by *B. cereus* lecithinase. According to Nygaard *et al.* (1954) and MacFarlane and Datta (1954), the destructive action of lecithinase on the succinoxidase system of rat- and mouse-liver mitochondria is due to phospholipid breakdown. Heimpel and Harvey (unpublished data) demonstrated that the *B. cereus* lecithinase completely blocks the succinoxidase system of mouse-liver mitochondrial preparations. A similar action on the mitochondria of insects infected with *B. cereus* might be postulated.

<sup>1</sup>Contribution No. 373, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

TABLE I — The Relative Virulence of Various Strains of *Bacillus cereus* when Ingested by Insects.

Insect tested	Virulence	Authority
Coleoptera		
<i>Rhizopertha dominica</i> F.	O L	Steinhaus and Bell (1953)
<i>Sitophilus oryzae</i> (L.)	(++)L	" " " "
<i>S. granarius</i> (L.)	(+)L	" " " "
<i>Tribolium confusum</i> Duv.	(+) to (++)L	
Hymenoptera		
<i>Neodiprion banksianae</i> Rohwer	(++)L	Heimpel (unpubl.)
<i>N. lecontei</i> Fitch	(++)L	Heimpel (unpubl.)
<i>N. sertifer</i> (Geoffr.)	(+)L	Heimpel (unpubl.)
<i>Pristiphora erichsonii</i> (Htg.)	(+++ )L to (++)F	Heimpel (1954)
Lepidoptera		
<i>Aphomia gularis</i> (L.)	O L	Steinhaus (1954)
<i>Carpocapsa pomonella</i> L.	(+++ ) L and F	Stephens (1952)
<i>Colias philodice eurytheme</i> Boisd.	O to (+) L	Steinhaus (1954)
<i>Ephestia kuehniella</i> Z.	O L	Heimpel (unpubl.)
<i>Gnorimaschema operculella</i> Z.*	(+)L	Toumanoff and Grison (1954)
<i>Junonia coenia</i> Hüb.	O L	Steinhaus (1954)
" "	O L	" "
<i>Malacosoma disstria</i> Hbn.*	(+) to (+++ )L	Toumanoff (1953)
<i>M. neustria</i> L.**	(+) to (+++ )L	Toumanoff (1953); Toumanoff and Grison (1954)
<i>Peridroma margaritosa</i> Hawworth	O L	Steinhaus (1954)
<i>Phygania californica</i> Packard	O L	Steinhaus (1951a)
<i>Pieris brassicae</i> (L.)*	(+++ ) to (++++ )L	Toumanoff (1953); Toumanoff and Grison (1954)
<i>Plodia interpunctella</i> Hbn.	O L	Steinhaus (1954)
<i>Prodenia praefica</i> Grote	O L	Steinhaus (1951a)
<i>Pyrausta nubilalis</i> Hbn.	O L	McConnell and Cutkomb (1954)
<i>Thaumatopoea processionea</i> Linn.*	(+++ )F	Grison and Beguin (1954)
<i>Thaumatopoea pityocampa</i> Schiff***	(+) to (+++ )L	Toumanoff (1953)
" " " *	(++)F	Grison and Beguin (1954)

L = Laboratory Tests

F = Field Tests

+ = 25% mortality (accumulative)

O = Non-pathogenic

\**B. cereus* (strain P-3) — Toumanoff

\*\**B. cereus* var. *galechiae* — Toumanoff

\*\*\**B. cereus* var. *cazaboun* — Toumanoff

There is good evidence that lecithinase plays a role in the invasion and destruction of insect tissues infected with strains and varieties of *B. cereus*. The conditions that promote the action of this enzyme in the group of susceptible insects and the extent to which it contributes to the virulence of *B. cereus* pathogens remains to be determined.

B. CEREUS STRAINS PRODUCING CRYSTALLINE INCLUSIONS

Some *Bacillus* species produce "para-sporal bodies", which are formed in the sporangium adjacent to the spore. They occur as crystalline inclusions in some species of the *B. cereus* 'group' and in certain other species such as *B. popilliae* Dutky, and *B. laterosporus* Laubach. It is interesting, but not necessarily significant in all cases, that these species are pathogenic for insects or are associated with them. Those not familiar with the occurrence or appearance of para-sporal bodies should consult Hannay's excellent review (Hannay, 1956).

The taxonomic position of those *B. cereus* isolates that produce crystalline inclusions is presently under debate. Smith *et al.* (1952) proposed that *Bacillus mycoides* Flügge, *Bacillus anthracis* Cohn, and *B. thuringiensis* should be reduced to varieties of *B. cereus*, because of their similarity to the parent species. Toumanoff (1952) proposed that a similar course be adopted for two silkworm pathogens, one referred to as *B. cereus* var. *alesti*, isolated in France, the other as *B. sotto* of Japanese origin. There are, however, consistent and recognizable differences between *sotto*, *thuringiensis*, and *alesti* (Toumanoff and Vago, 1955; Angus, 1956a).



Delaporte and Beguin (1955) make a somewhat different proposal in a paper on a spore-forming, crystal-producing aerobe pathogenic for silkworm larvae, which they identify as *B. thuringiensis*. Arguing that there are a number of differences between *B. cereus* and the other insect pathogens, the most important being the production of crystals, they propose that *B. thuringiensis* be retained as the "parent" species of the insect pathogens similar to *B. cereus*, even though *sotto* is an older name than *thuringiensis*. The situation is now complicated by the finding of Toumanoff and his colleagues (Toumanoff *et al.* 1955) that the *alesti* strain can be "dissociated" to a non-crystal-producing strain that can, under certain conditions, resume crystal production. Steinhaus and Jerrel (1954) and Angus (1956a) have recommended that the older names be retained pending further work. Hereafter in this paper, the older names will be used but it should be understood that *thuringiensis*, *sotto*, and *alesti* are very similar to each other and to *B. cereus*.

BACILLUS THURINGIENSIS BERLINER

*B. thuringiensis* was isolated from diseased flour moth larvae (*Ephestia kühniella* (Zell.)) and described by Berliner (1915), and studied by Mattes (1927). Steinhaus (1949, p. 278) has given a complete discussion of the work with this organism up to 1949. The large number of feeding tests carried out with this bacterium are summarized in Table II. It is worthy of note that *B. thuringiensis* is apparently a non-specific pathogen since it demonstrates virulence, albeit variable in intensity, for a wide variety of insects.

TABLE II — The Relative Virulence of Various Strains of *Bacillus thuringiensis* when Ingested by Insects.

Insect tested	Virulence	Authority
Coleoptera		
<i>Rhizopertha dominica</i> (Fabr.)	O L	Steinhaus and Bell (1953)
<i>Sitophilus granarius</i> (L.)	(++)L	" " " "
<i>S. oryzae</i> (L.)	(+++++)L	" " " "
<i>Tribolium confusum</i> Duv.	O to (+)L	" " " "
<i>Trogoderma granarium</i> Everts	O L	De and Konar (1955)
Hymenoptera		
<i>Pristiphora erichsonii</i> (Htg.)	(++)L	Heimpel (1955b)
Lepidoptera		
<i>Anisota rubicunda</i> (Fabr.)	(+++++)L	Angus (1956a)
<i>Anisota senatoria</i> (A. and S.)	(+++++)L	" "
<i>Colias philodice eurytheme</i> Boisd.	(+++++)L and F	Steinhaus (1954)
<i>Crambus bonifatellus</i> (Hulst)	(+++++)L and F	Hall (1954)
<i>Crambus sperryellus</i> Knots	(+++++)L and F	Hall (1954)
<i>Datana integerrima</i> (G. and R.)	(++) to (+++++)L	Angus (1956a)
<i>Harrisina brillians</i> B. and McD.	(+++++)L	Thompson and Logan (Hall (1955)
<i>Harrisina brillians</i> B. and McD.	(++) to (+++++)F	Hall (1955)
<i>Heliothis obsoleta</i> Fabr.	(+++++)L	Majumder. Muthie and Pingale (1955)
<i>Hellula undalis</i> (Fabr.)	(+) to (++)F	Tanada (1956)
<i>Junonia coenia</i> Hüb.	(+)L	Steinhaus 1954)
<i>Lambdina fiscellaria</i> (Guen.)	O L	Angus (1956a)
<i>Peridroma margaritosa</i> (Hawworth)	O to (+)L	Steinhaus (1951a)
<i>Phryganidia californica</i> Packard	(+)L	Steinhaus (1951a)
<i>Pieris brassicae</i> (L.)*	(+++++)F	Delaporte and Beguin (1955)
<i>Pieris rapae</i> (L.)	(+++++)L	Tanada (1953)
" "	(+++++)F	Tanada (1956)
<i>Plutella maculipennis</i> (Curt.)	(+++++)F	Tanada (1956)
<i>Prodenia praefica</i> Grote	(+)L	Steinhaus (1951
<i>Sitotroga cerealella</i> (Oliv.)	(+++++)L(?)	Steinhaus and Bell (1953)
<i>Thaumotopea pytiocampa</i> Schiff.	(+++++)F	Grisson and Beguin (1954)
<i>Trichplusia ni</i> (Hbn.)	(+) to (++)E	Tanada (1956)

L = Laboratory Tests  
+ = 25% mortality (accumulative)  
F = Field Tests  
O = Non-pathogenic

\**B. thuringiensis* (anzube strain)



Angus (1956a) has shown in quantitative tests that *B. thuringiensis* is 10 to 20 times less virulent for silkworm larvae than is *B. sotto*. This difference may be due to the fact that *thuringiensis* toxin is not as soluble as *sotto* toxin at pH 10.2.

#### BACILLUS SOTTO ISHIWATA

*B. sotto* was isolated from diseased larvae of the silkworm, *B. mori*, and described by Ishiwata. Sporulated cultures of it cause paralysis in and death of silkworm larvae; because they could not detect bacterial growth in affected larvae, Aoki and Chigasaki (1915a) suggested that the paralytic action was due to a pre-formed toxin, which they were unable to isolate or identify. Sporulated cultures of *B. sotto* contain crystalline inclusions similar to those found in *B. thuringiensis* (Hannay and Fitz-James, 1955), and the toxic action is believed to be due to a proteinaceous compound associated with the crystals. A toxin has been extracted from cultures of *B. sotto*, the LD<sub>50</sub> of which is about 0.5 µg per gram of larva for silkworms. The extract is also toxic for some other lepidopterous larvae that have highly alkaline mid-gut contents. One of the effects of the toxin is a marked increase in the alkalinity of the blood of affected silkworm, and this change parallels the onset of paralysis symptoms. This work has been described in detail in a number of recent papers (Angus, 1954; 1956a, b, c, d; Angus and Heimpel, 1956).

#### *B. cereus* var. *alesti* TOUM. AND VAGO

*B. cereus* var. *alesti* is another of the crystal-producing entomogenous *Bacillus* strains that attack larvae. It was first isolated from dead silkworm larvae in France (Toumanoff and Vago, 1951) and is the causal agent of an endemic flacherie, which occurs in the Cévennes area. The epidemiology of the disease, the symptoms, and the causal agent have been reported on in a number of papers since 1951 (Vago, 1951; Toumanoff and Vago, 1951, 1952a, b, c, 1953a, b, 1955; Toumanoff 1952, 1955; Toumanoff and Lapied, 1954; Toumanoff *et al.*, 1954, 1955; Toumanoff and Virat, 1955). The work with *alesti* preceded that with *sotto*, but the latter has been discussed first because it helps in understanding the *alesti* results.

Toumanoff and Vago (1953) noted that death of larvae affected with *B. cereus* var. *alesti* could be due to toxemia, septicemia, or intermediate conditions. Old sporulated cultures cause a rapid paralysis or toxemia, whereas young cultures cause a slow morbid septicemia. The histopathology of the disease caused by the *alesti* variety was also studied in some detail and it was concluded that the toxic action of *alesti* was due to a substance, elaborated in the course of bacterial metabolism, that fixes on the bacterial cell and is probably found with the spores and liberated by the bacillus under the effect of lysis. At the time of publication, the presence of crystalline inclusions in *B. cereus* var. *alesti* was not suspected. When the results of the work with *alesti* are compared with the *sotto* findings, it is obvious that very similar systems are present.

In addition to histopathological studies, the effect of the *alesti* disease on silkworm has been studied by Drilhon and Vago (1953) as a problem in physiology. They found that changes in the level of amino acids and fluorescent substances in the blood of affected larvae parallel the development of the paralysis caused by the *alesti* strain. These biochemical changes can be correlated with the histological findings, but Drilhon and Vago do not exclude the possibility that bacteria in the gut were responsible for the changes in haemolymph components.

Toumanoff, Vago and Gladiline (1954) published a paper on the pathogenicity for silkworm larvae of young and old, broth and agar cultures of *B. cereus* var. *alesti* treated in various ways. More recent work in North America (Steinhaus, 1954; Heimpel, 1954, 1955b; and Angus, 1956c) with *B. cereus* and *B. sotto* suggests that this earlier paper of Toumanoff *et al.* is concerned with the interaction of a water-soluble lecithinase of the vegetative phase of growth and a water insoluble protein from the crystalline inclusions which occur in sporulating cells.

The most recent paper dealing with *B. cereus* var. *alesti* (Toumanoff, 1955) also deals, in part, with the possible action of lecithinase. In it Toumanoff considers lecithinase to be one of the factors involved in the *alesti* disease.

Summaries of feeding tests using *B. cereus* var. *alesti* and *B. sotto* are given in Tables III and IV respectively.

TABLE III — The Relative Virulence of *B. cereus* var. *alesti* when Ingested by Insects.

Insect tested	Virulence	Authority
<i>Bombyx mori</i> L.	( + + + + ) L	Toumanoff and Vago (1952a)
<i>Galleria mellonella</i> (L.)	( + + ) to ( + + + ) L	Toumanoff (1954a)
<i>Gnorimoschemia operculella</i> Zell.	( + + + ) L	Toumanoff and Grison (1954)
<i>Hybonomeuta cognatella</i> Hab.	( + + + ) L	Toumanoff (1954)
<i>Hyponomeuta padella</i> Hub.	( + + + + ) L	Toumanoff (1955)
<i>Malacosoma neustria</i> L.	( + + + ) to ( + + + + ) L	Toumanoff (1955); Toumanoff and Grison (1954)
<i>Pieris brassicae</i> (L.)	( + + + + ) L	Toumanoff and Grison (1954)

L=Laboratory Tests

F=Field Tests

+ = 25% mortality (accumulative)

O = Non-pathogenic

TABLE IV — The Relative Virulence of *B. sotto* when Ingested by Insects.

Insect tested	Virulence	Authority
Lepidoptera		
<i>Anisota rubicunda</i> (Fabr.)	( + + + ) to ( + + + + ) L	Angus (1956a)
<i>Anisota senatoria</i> (A. and S.)	( + + + ) to ( + + + + ) L	" "
<i>Bombyx mori</i> L.	( + + + ) to ( + + + + ) L	" "
<i>Choristoneura fumiferana</i> (Clem.)	O L	Angus (1956d)
<i>Cirphis unipuncta</i> (Haw.)	O L	" "
<i>Datana integerrima</i> (G. and R.)	( + + + ) to ( + + + + ) L	Angus (1956a)
<i>Datana ministra</i> (Drury)	( + + + ) to ( + + + + ) L	" "
<i>Erranis tiliaria</i> (Harr.)	( + + + ) to ( + + + + ) L	" "
<i>Galleria mellonella</i> (L.)	O L	Angus (1956d)
<i>Nymphalis antiopa</i> (L.)	( + + + ) to ( + + + + ) L	Angus (1956a)
<i>Porthetria dispar</i> L.	( + + + ) to ( + + + + ) L	" "
<i>Protoparce quinque maculata</i> (Johan.)	( + + + ) to ( + + + + ) L	" "
<i>Protoparce sexta</i> (Haw.)	( + + + ) to ( + + + + ) L	" "
Hymenoptera		
<i>Diprion hercyniae</i> (Htg.)	O L	Angus (1956d)
<i>Neodiprion abietis</i> Harris	O L	" "
<i>Neodiprion americanus banksianae</i> (Roh.)	O L	Angus (1956d)
<i>Neodiprion lecontei</i> Fitch	O L	Heimpel (unpubl.)
<i>Neodiprion sertifer</i> (Geoff.)	O L	Angus (1956d)
<i>Pikonema alaskensis</i> (Roh.)	O L	Heimpel (unpubl.)
<i>Pristiphora erichsonii</i> (Htg.)	( + + ) L	Heimpel (unpubl.)

L=Laboratory Tests

F=Field Tests

+ = 25% mortality (accumulative)

O = Non-pathogenic

FACTORS AFFECTING THE MODE OF ACTION OF ENTOMOGENOUS BACTERIA

In most cases of bacterial infections in insects, the portal of entry is the digestive tract, and multiplication of the pathogen in the larval gut precedes the appearance of symptoms. This is not true, of course, for the toxemias caused by the crystal producers. The conditions in the digestive tract may exert a great influence on any bacteria taken in with the food. The presence of anti-bacterial substances or of unfavourable growth conditions, such as extremes of pH, might make the development and multiplication of the ingested bacteria difficult or impossible.

Should the conditions in the digestive tract be favourable for spore germination and multiplication, the bacteria may invade the blood and if they or their soluble toxins reach the blood, there are still several obstacles to overcome. Blood cells of many insects are capable of active phagocytosis; there is also the possibility that humoral immunity might hinder bacterial growth and/or neutralize toxins entering the blood. Usually,

multiplication of bacteria in the blood results in death of the host. Antibiotics might possibly halt this process, although there is no case cited in the literature where it has been adequately demonstrated that an antibiotic in the blood protects the insect after bacteria have invaded the haemocoel from the digestive tract. Possibly the damage done to the gut in most cases of invasion is irreparable.

THE SIGNIFICANCE OF pH IN BACTERIAL DISEASES OF INSECTS

The hydrogen-ion concentration in the insect gut is one of the major factors governing the extent of multiplication and the mode of action of some bacterial entomophytes. Many studies have been made of the pH in the tissues of various insects, fortunately most of the information can be found in recent reviews and papers (Staudenmeyer and Stellwaag, 1940; Waterhouse, 1949; Grayson, 1951; Roeder, 1953; Roeder, 1953 p. 182; Heimpel, 1955c, 1956). Very little use has been made of pH measurements as a diagnostic tool in insect pathology and most published values are those of healthy insects. Many of the earlier results are for the whole digestive tract and were obtained by using a variety of methods. With the introduction of single-drop glass electrodes and electronic meters, greater accuracy in measuring small samples has been achieved; consequently some of the earlier published values may require amendment.

Most of the recent studies with “*B. cereus* group” organisms have been made with Lepidoptera and Hymenoptera and readings have been made of the various anatomical regions of the digestive tract and of the blood of the insects from these two orders (see Table V).

TABLE V — A Comparison of the Relative pH Values of the Blood and Gut of Larvae Belonging to the Orders Lepidoptera and Hymenoptera.

Order	Type	Blood pH	Blood Variation in pH units	Crop pH	Midgut pH	Hindgut pH
Lepidoptera	I	5.60-7.56	1.96* 0.2**	6.59-10.40	8.5-10.7	4.01-7.88
	II	5.60-7.0	1.40* 0.2**	6.50-8.34	6.40-9.25	5.90-7.80
Hymenoptera		6.35-7.33	0.98* 0.2**	5.1-7.7	6.14-9.63	5.44-7.32

\*Interspecific variation  
\*\*Intraspecific variation

In Lepidoptera, there is considerable variation in the pH of the gut contents. There exist at least three types of insects easily distinguishable in this respect. Type I, represented by such insects as *B. mori* and *Anisota senatoria* (A. and S.), has a strongly alkaline midgut, whereas Type II Lepidoptera have midgut contents closer to neutral, e.g. *Choristoneura fumiferana* (Clem.), *Carpocapsa pomonella* (L.), and *E. kühniella*. Type III larvae represented by three species of *Malacosoma*, i.e. *M. americanum* (Fabr.), *M. disstria* Hbn., and *M. pluviale* (Dyar) are similar to those of Type I, however they do not feed continuously but alternate the feeding periods with periods of rest, and it has been noted that the pH of the crop and of the gut varies with this feeding cycle<sup>2</sup>.

The hydrogen-ion concentration in the gut contents may also vary considerably depending on the condition of the insect. Inanition, ecdysis, and pupation are among the factors causing changes in pH (Roeder, 1953, p. 329).

The blood of Lepidoptera is considerably less variable (inter- and intra-specifically) than is the gut content. Although metamorphic changes tend to increase the hydrogen-ion concentration of the blood (Roeder, 1953, p. 216), it appears that Lepidoptera can tolerate change to the acid side better than change to the alkaline side. A reduction in hydrogen-ion concentration of 1.2 pH units in the blood of *B. mori* causes paralysis leading to death; a concomitant increase in hydrogen-ion concentration of the gut contents has been noted in larvae fed either sporulated *sotto* cultures or toxin derived

<sup>2</sup>In *M. pluviale* the crop may vary from pH 6.8 to pH 9.3 depending on whether the insect is feeding or resting respectively. The median portion of the midgut may vary from pH 10.3 to pH 9.0 under the same conditions.

from sotto cultures. The symptoms preceding the characteristic paralysis in affected larvae can be correlated with the changes in pH (Angus and Heimpel, 1956). This relationship is shown in Fig. 1.

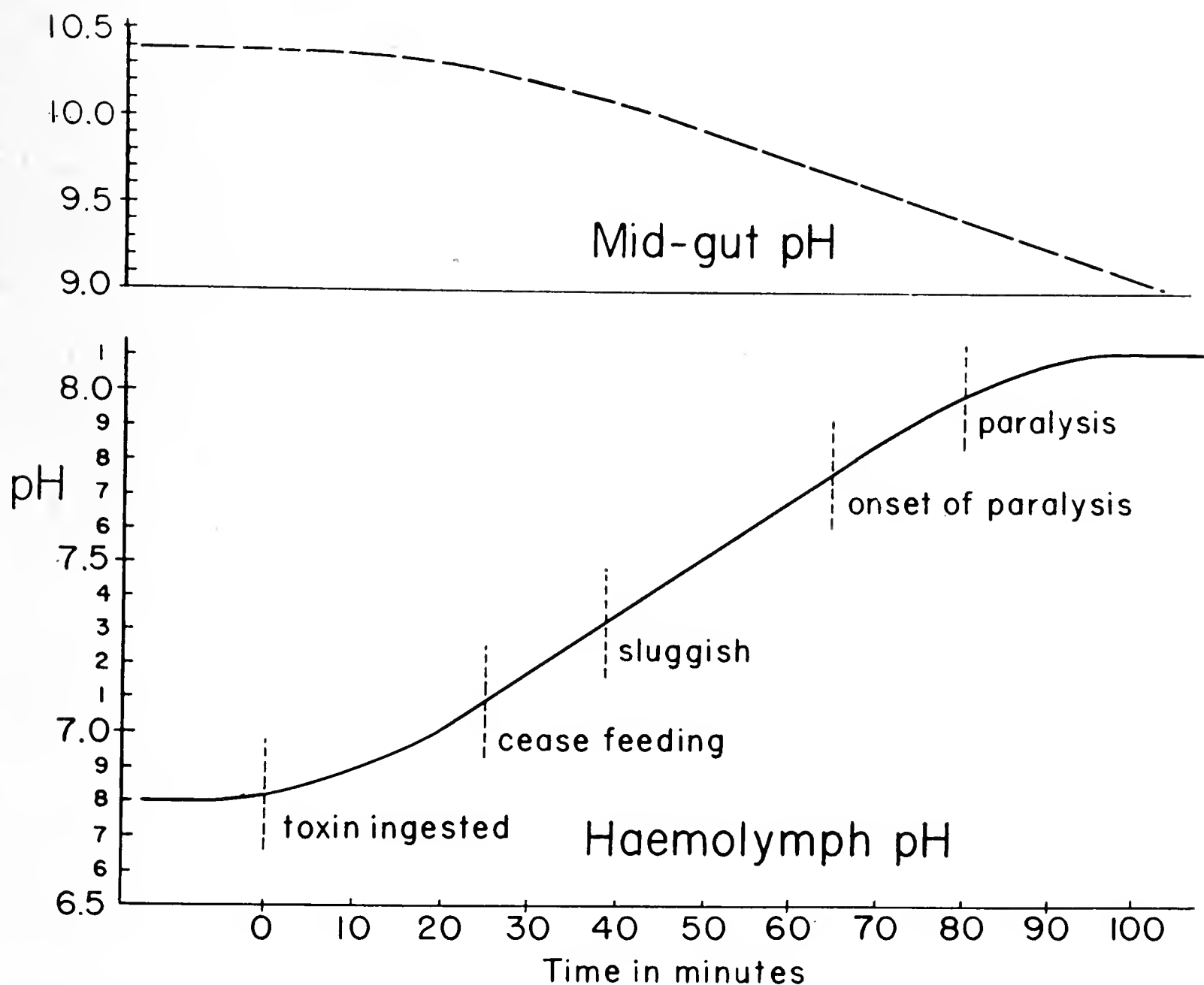


Fig. 1. Effect of *B. sotto* toxin on *B. mori* larvae.

Only a few reports on the pH conditions in larvae of phytophagous Hymenoptera are available. Generally, those species examined have a lower pH in the midgut than do most Lepidoptera (Grayson, 1951; Heimpel, 1955c, 1956). The pH of the midgut contents should allow good bacterial growth and, significantly, several species of sawflies are susceptible to infection by strains of *B. cereus* and by *Serratia marcescens* Bizio (Heimpel, 1955a). These bacteria do not demonstrate the same degree of pathogenicity for Lepidoptera with strongly alkaline midguts. The pH of the blood of sawflies lies within the pH range of most other insects. The interspecific variation in last instar sawfly larvae of all species examined is very low (0.98 pH units) and the intraspecific variation is less than 0.2 pH units.

#### ANTIBIOTIC OR ANTI-BACTERIAL SUBSTANCES IN INSECTS

It has been known for some time that insects produce substances that inhibit the growth of certain kinds of bacteria, but we know of no cases where it has been demonstrated that such a mechanism operates effectively against an entomogenous bacterium. From the time of Glaser (Glaser, 1918), there have been many reports of anti-bacterial substances in insects but space does not permit detailed mention of them (Eckstein, 1931; Hindle and Duncan, 1925; Violle and Sautet, 1938; Oliver, 1947; Rehm, 1948; and Pavan, 1950).

#### BACTERIAL IMMUNITY IN INSECTS

The literature on insect immunity has been reviewed by Steinhaus (1949), and unfortunately only a few investigators have recently done work in this field. Paillot (1933, p. 202) supported the view that humoral agents are mainly responsible for



resistance. On the other hand, a review was published by Toumanoff (1949) laying emphasis upon the phagocytic action of blood cells as the major factor in the response of insects to a bacterial infection. It becomes obvious that a great deal of careful research is required in this field before the question is settled. However, it may be assumed that both cellular and humoral immunity exist in insects, and their relative importance varies depending upon the species of bacterium and the species of insect involved.

Briggs recently completed serological studies involving 11 species of Lepidoptera, including *B. mori* and reported these findings at this Congress. Live and attenuated suspensions of bacteria (both pathogens and non-pathogens of insects), viral suspensions, and solutions of ovalbumin (2 x crystallized, salt free) were used as particulate and soluble antigens respectively. Antigens were injected into the haemocoel of experimental larvae except in the case of virus antigens which were fed to the larvae. Serological techniques, such as agglutinin, precipitin, and complement-fixation tests, were not adaptable for demonstration of natural or acquired immune properties in the haemolymph of lepidopterous larvae. Diphtheria antitoxin reactions were not demonstrable in vaccinated larvae.

A relatively non-specific increase in tolerance to the minimum lethal dose of pathogenic bacteria was acquired by larvae infected with various live and attenuated bacterial suspensions. A demonstrable immunological response was achieved only upon the injection of materials into the larval body cavity. This increase in tolerance was found to be parallel to the rise of an extremely heat-stable, anti-bacterial principle, demonstrated *in vitro*, in the sera of insects a few hours after vaccination. The acquired anti-bacterial property in larval haemolymph was shown to be rather non-specific in its action, to be retained throughout larval life, to resist exposure to acid and alkali, but to be eliminated when exposed to the action of pepsin.

The thermostability of this anti-bacterial principle tends to set it apart from vertebrate anti-bodies in the light of our present knowledge. Briggs suggests this does not disprove its protein nature for it might represent a case of a system in which the antibody is protected from prolonged exposure to heat by inorganic or organic constituents characteristically present in insect blood (e.g. the great amounts of magnesium or the high concentration of amino acids).

### GENERAL REMARKS

From the foregoing it is obvious that much of the research to date has been concerned with the isolation of new pathogens or the testing of known entomogenous strains against various insects. As indicated in the preceding tables, the *B. cereus* entomogenous strains attack a large number of species and it is likely that this list is not yet complete.

The *B. cereus* 'group' has received a great deal of attention lately and sufficient knowledge has been accumulated to indicate that earlier theories on the mode of action of the species in this group may require modification. The histopathology of various *B. cereus* group diseases of insects provides some very useful hints in this respect. In 1915, Berliner reported that *B. thuringiensis* growing in the gut of *E. kühniella* larvae damaged it, causing erosion of the cells, with resulting breakthrough of the bacteria into the haemocoel. However, Mattes, in 1927, confused the picture by reporting that *B. thuringiensis* penetrates between the cells without eroding the gut. To explain the fact that this was rarely observed, he claimed that the penetration of bacteria must be very rapid. One of us (A.M.H.) has repeated Mattes' histological work, using his strain of *thuringiensis*, but the type of penetration seen by Mattes was never encountered. However, the type of penetration of the gut described by Berliner was seen frequently by Tanada (1953) in *Pieris rapae* (L.) by Toumanoff and Vago (1953a) using *B. cereus* var. *alesti* and the silkworm, and by Heimpel (1954) in the larch sawfly. This ability of *B. cereus* group bacteria to loosen and/or destroy the midgut cells suggests that a substance capable of breaking down the cell-cementing substances is produced. Day and Powning (1949) showed that hyaluronidase separates the epithelial cells of *Blatella germanica* (L.), and it is possible that some such enzymatic action is involved in *B. cereus* invasion. The histopathological studies show us that the



first tissue injured (and apparently irreparably so) is the midgut. It might be postulated that this is the primary and important stage, all other action, including the septicaemia, being secondary in importance.

Reference has been made to the observation, confirmed by several workers, that young cultures of certain *B. cereus* strains may cause death if ingested by certain insect larvae. In all cases death is caused by active growth of the bacterium in the gut and eventually in the blood. However, work with *B. mori* larvae has shown that ingested *Bacillus* spores do not germinate in the silkworm gut and further that young cells, if ingested with food, are killed or destroyed in the gut (Aoki and Chigasaki, 1951a). This is true also of larvae of certain other Lepidoptera. In all such species having decidedly alkaline mid-gut contents, it may be that spores are incapable of successfully germinating or vegetative cells of surviving in such an environment. There are lepidopterous and hymenopterous larvae whose mid-gut contents are only slightly alkaline, and in these species *B. cereus* spores germinate and their vegetative cells multiply rapidly. Phospholipase C is an enzyme associated not with sporulation or spore germination but with the logarithmic phase of vegetative growth, and in addition its optimal pH range coincides very closely with the gut pH of those insect species in which vegetative cells of *B. cereus* survive and multiply (Heimpel, 1955b). This indicates that the pH of the gut contents is an important factor in host-parasite relationships.

*B. mori* larvae become paralyzed following ingestion of sporulated cultures of the *alesti*, *sotto*, or *thuringiensis* strains. If sporulated cultures of these species are extracted with gut juice or dilute alkali solutions, a paralyzing sterile extract can be obtained (Angus, 1954, 1956b, c). The mid-gut contents of *B. mori* are strongly alkaline, and it is the most susceptible insect known to the action of the proteinaceous component of the crystals found in sporulated *sotto* cultures. Other susceptible species of insects have quite alkaline mid-gut contents, and this also suggests a causal relationship between susceptibility and pH of mid-gut contents; that is, an insect may not be affected by the toxic protein associated with the crystals unless the mid-gut contents are sufficiently alkaline to dissolve the crystal or some part of it.

It should be possible, in the present state of our knowledge, to be more rational in our choice of hosts for testing entomogenous bacteria. The negative results obtained in many cases may be indicative of an uninformed choice of host rather than an inferior pathogen.

Thus there are at least two toxin systems in the *B. cereus* 'group': one is derived from young cultures and is due to phospholipase C; the other is associated with the crystalline inclusions found in sporulated cultures of certain strains. These systems have been studied separately in some detail, but it is probable that in nature the two systems are linked, the one preparing the way for the other. In laboratory tests, it has been shown that there is a minimum lethal dose of *sotto* toxin and that toxin-free spores are without effect even if  $10^7$  spores per insect are ingested. In nature, spores and crystals (from which the toxin is derived) occur together. It is not known what happens if a sub-lethal dose of crystals or toxin is ingested together with a small quantity of spores.

In Table VI we have attempted to summarize our present knowledge of the *B. cereus* entomophytes. Table VI (A and B) gives the details of the action of both crystal-forming and non-crystal-forming species of the *B. cereus* group on susceptible insects. Table VI (B and C) provides further theoretical considerations concerning the action of these bacteria; it differs from the demonstrated facts, in the previous table, in two ways. First, in insects with midgut contents over pH 9.0, there may be some action by exotoxins, especially if the insect is placed under stress that causes a lowering of the mid-gut pH, thus possibly allowing germination and multiplication of vegetative cells. This might permit the action of the exotoxin to take place, particularly when sub-lethal doses of the endotoxin are ingested.

In this form the picture seems to be reasonably well integrated. There is one anomaly. When a sporulated culture of *B. thuringiensis* is ingested by *E. kühniella*, the larvae die of septicemia after 30-36 hours without any preliminary paralysis. From

TABLE VI — Mode of Action of *B. cereus* Entomophytes. Known: A and B.  
Postulated: A and C.

	A			B			C		
	Gut contents- <u>under</u> pH 9.0			Gut contents- <u>over</u> pH 9.0			Gut contents- <u>over</u> pH 9.0.		
	Cell growth	Exotoxin active	Endotoxin active	Cell growth	Exotoxin active	Endotoxin active	Cell growth	Exotoxin active	Endotoxin active
Young cultures (vegetative cells)									
Sporulated cultures							secondary		primary
Filtrates of young broth cultures (concentrated)									
Intact crystals or solution of crystals									
<div><div>B.cereus - </div><div>B.sotto or alesti - </div><div>Both species - </div></div>									

our knowledge of the conditions under which *thuringiensis* crystals can be dispersed *in vitro* (pH 12.2: Hannay and Fitz-James, 1955), it appears that the crystals could not be dissolved in the gut of *E. kühniella* larvae (pH 6.8-8.4). Presumably then, the crystals are inert in this instance and death is due to some activity of the vegetative cells following spore germination (excluding the possibility that the crystal is activated or made soluble by some enzyme normally in the *kühniella* gut). Further, if spores of a non-crystal-forming strain of *B. cereus* are fed to *E. kühniella*, they germinate and multiply, but only slowly. Often one may find in the mid-gut, clumps of bacteria that apparently are disintegrating, leaving only basophilic granules behind. The bacteria, however, are not able to kill the insect. This excludes the possibility that lecithinase alone is responsible for the death of *E. kühniella*.

There are at least three theories currently under investigation at Sault Ste. Marie concerning this insect and *B. thuringiensis*: (1) There is a possibility that *B. thuringiensis* may produce an undetected toxic substance that is not produced by *B. sotto* or by members of the *B. cereus* group; (2) There may be a mechanism of releasing the crystal toxin other than solution at high alkalinity; (3) Since *B. thuringiensis* is more resistant to anti-biotics than are *B. cereus* strains, it might be that the *kühniella* larvae possess an anti-bacterial substance that discourages all *B. cereus* 'group' species but not the closely allied *B. thuringiensis*.

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# Humoral Immunity in Lepidopterous Larvae

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## ABSTRACT<sup>1</sup>

*The larvae of eleven species of Lepidoptera were used as experimental insects. Live and attenuated suspensions of bacteria (pathogenic and non-pathogenic for insects) and solutions of ovalbumin were used as particulate and soluble antigens respectively. Antigens were injected into the hemocoels of experimental larvae except in limited cases where virus antigens were fed to the larvae.*

*Serological techniques, such as agglutinin, precipitin and complement-fixation tests, were found not to be adaptable for demonstration of natural or acquired immune properties in the hemolymph of lepidopterous larvae. Diphtheria antitoxin reactions were not demonstrable in vaccinated larvae. A relatively non-specific increase in tolerance to the minimum mortal dose of species of pathogenic bacteria was shown to be acquired by larvae injected with various live and attenuated bacterial suspensions. This increase in tolerance was found to parallel the rise of an extremely heat stable antibacterial principle, demonstrated in vitro, in the sera of insects a few hours after vaccination. A demonstrable immunological response was achieved only upon injection of materials into the body cavity of the larvae, never by feeding of the inoculum.*

*The possible similarity of the antibacterial principle in larvae of Lepidoptera to the vertebrate serum protein properdin was investigated.*

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# Stress as a Factor in Insect Disease

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## ABSTRACT

*The phenomenon of latency in insect viruses is one aspect of a broader field of endeavor that we are investigating in our laboratory. Our approach to the problems involved (and covered by this symposium) is from the standpoint of attempting to understand the relation between disease and certain stressors and incitants. We are presently, or expect to be, concerned with approximately twenty different types of stressors (e.g., crowding, heat, cold, chemicals, nutrition, radiation, etc.) and their role in the manifestation of disease in insects. This report presents a brief summary of some of the results gathered from preliminary experiments along these lines.*

By the beginning of the nineteenth century, most of those who observed that the silkworm suffered from diseases recognized that environmental factors influenced the course of these maladies to a greater or lesser extent. Prior to the advent of the germ theory of disease, sericulturists considered such influences to be the actual cause of the diseases. As it became known that most of the maladies that ravaged the silkworm nurseries of Europe and the Orient were caused primarily by microorganisms, the various environmental influences were considered to be factors that sometimes aggravated the diseases or predisposed the insect to them, or otherwise activated the disease processes involved.

While it is generally recognized that such factors as crowding, excessive heat and humidity, and abnormal nutrition may tend to promote the outbreak of certain diseases in certain insects, there is, in general, surprisingly little specific information or detailed data on their relation to disease, and there is a great paucity of information on most other factors that may predispose insects to disease, or in some way make them more susceptible to attack by living microorganisms, or activate disease within them. Nevertheless, enough is known to indicate that with insects, as with other animals, there is some relation between environmental stress and disease.

The importance of this matter from an epizootiological point of view is frequently apparent in observing the natural occurrence of disease in insect populations. In the course of our study of virus-caused epizootics in populations of the alfalfa caterpillar, for example, we have been impressed by the fact that the disease appears to break out in all parts of an alfalfa field at about the same time. Rarely does the disease appear first in the caterpillars of one corner or segment of the field, and then extend gradually to the insects in the remainder of the field. Instead, larvae throughout the field are in essentially the same stage of disease at the same time. It is as though the virus were already well distributed among the caterpillars, or had remained latent within the insects, until it was activated by some general environmental influence or stress.

The role of stress in the diseases of man has long been recognized. The works of Selye (1950, 1952, 1955) and others during the past two decades has offered a new approach to some of the problems of medicine. The central core of Selye's concepts has to do with the endocrine system and its response to various stressors. The relationship between the "general-adaptation syndrome" or "stress syndrome" and various human diseases is under intensive study in different parts of the world. It cannot be assumed that the mechanisms involved in stress-induced diseases in man are the same as those operating in insects, but that stress does play a role in the occurrence of disease in insects seems clear. While the effect of stressors upon the hormone systems of insects is not outside the scope of our present studies, it is apparent that certain preliminary and somewhat less involved matters with regard to the role of certain stressors in insect disease might well be examined first.

In our laboratory we have sought to approach such problems as those concerned with virus latency, for example, from the standpoint of trying to understand the relation between disease and certain stresses. Among the stressors we are now studying,

or expect to study in the future, are: 1. Crowding; 2. Administration of certain chemicals and drugs; 3. Excessive heat; 4. Excessive cold; 5. Excessive atmospheric humidity; 6. Excessive drought; 7. Starvation; 8. General abnormal nutrition; 9. Specific nutritional deficiencies; 10. Excessive moisture in food; 11. Lack of oxygen; 12. Hormone imbalance (including administration of hormones); 13. Protein intoxication; 14. Solar radiation (ultra-violet light); 15. X-rays; 16. Physical injuries (e.g., wounds, blood-letting, feeding of abrasives, electrical injury, etc.); 17. Hyperactivity (excessive physical exercise).

It is obvious that the experimental variation with which each of these stressors may be studied is great. Not only does each stressor vary as to intensity (or degree) and timing, but when applied to the test insects they must be studied in relation to the insect's age, instar, stage, sex, species, etc.

The meaning of the word "stress", as used in this paper, is probably self-evident. The term is used simply to refer to any adverse force or condition, strain, pressure, or inconvenience to which the insect is subjected, and which conceivably might make it more prone to disease. To be sure, some stresses, of sufficient intensity or length of application, might in themselves be the cause of noninfectious disease concerned with deranged metabolism or abnormal physiology. Our interest, however, is not in the direct effect of stress, but the role that stress might play in the inducement, elicitation, provocation, or activation of an infectious process or disease. Included in our consideration of stress phenomena is the effect that certain stressors may have on the course of disease incited by the intentional infection of the insects concerned.

Although no thorough effort to do so is made in this paper, a distinction should be made between an infectious disease that results from the effects of stress on the innate resistance and strength of the host insect, and a disease that results from the effects of stress on the infectious agent itself, activating it so that it initiates or sets up a disease process in an otherwise normal or healthy host. In our present state of inadequate knowledge we cannot readily divide agencies into those which permit infection or disease by weakening the insect, and those which do so by stimulating or activating the pathogen or potential pathogen. Nevertheless, it is to be hoped and expected that eventually we shall be able more clearly to discern between these two types of action which, of course, may at times occur simultaneously or overlap in their effects. It would appear desirable to limit the term "stress" to mean a force that acts on or through the host organism, and to use another term (e.g., "incitation") in referring to the stimulation or activation of the infectious agent involved. The agencies themselves might be referred to as "stressors" on the one hand, and "incitants" on the other. The word "stress" might also, of course, be used as a verb in referring to the application or subjection of an insect to the action of the external forces concerned.

It should be mentioned that one practical objective involved in an investigation of this kind has to do with the use of microorganisms in the biological control of harmful insects. Without going into detail, it may be pointed out that one of the greatest drawbacks to the more extensive use of microbial control methods is our ignorance of the effects of the various environmental factors concerned. Furthermore, outbreaks of natural epizootics in insect populations appear to be initiated and governed not only by obvious meteorological factors but by other basic and little understood influences as well. It appears likely that in many cases effective microbial control will be reliably attained only after it is learned how to manipulate these factors. Then too, it is not impossible that if, as some believe to be true with certain virus infections, disease can be induced by the feeding of certain common chemicals, effective control methods may be developed through the application of stressors (or incitants) or by the combination of the application of stressors and pathogens.

## EXPERIMENTATION

Our investigation of the effects of stress on insects in relation to their diseases has been underway for the past several years, with considerable intensification of the work since 1954<sup>1</sup>. During this time we have performed a large number of experiments and

<sup>1</sup> The experimentation involved in this investigation is being supported by a grant from the U. S. Public Health Service, Grant No. E-1000.

have accumulated great quantities of data. We have learned a number of unexpected things in doing this type of work, one of them being that the results are extremely difficult to interpret with confidence. For this reason, and because of insufficient time, I am not prepared on this occasion to present the detailed results of our work, or to offer any final interpretation of them. I should, however, like to offer a few tentative, general impressions that have been gained from the results so far accumulated.

It is obvious that the nature of the results obtained in any particular type of stress experiment would depend on or be affected by the type of insect involved. Because of their availability, and because they are known to be susceptible to a variety of diseases, the insects used in our experiments have been limited primarily to the silkworm, *Bombyx mori* (Linnaeus) [Bombycidae], and larvae of the following "wild" species: the buckeye caterpillar, *Junonia coenia* Hübner [Nymphalidae], the variegated cutworm, *Peridroma margaritosa* (Haworth) (= *Peridroma saucia* Hübner) [Phalaenidae], the alfalfa caterpillar, *Colias philodice eurytheme* Boisduval [Pieridae], the California oakworm, *Phryganidia californica* Packard [Dioptidae], and the omnivorous looper, *Sabulodes caberata* Guenée [Geometridae]. In most of our experiments laboratory-reared specimens of these species were used, although in some instances field-collected material was utilized.

I should like to make it clear that the general description of results and interpretations included in the present paper are based on and apply only to the insects listed in the preceding paragraph. Even with these species we feel that generalizations, on the basis of the results we have obtained, are premature.

#### CROWDING AS A STRESSOR

On the basis of a large number of experiments of different types, but designed specifically to test the effects of crowding on the insects concerned, we can confirm the general impression that the greater the number of insects that are confined to a given space, the greater is the incidence of spontaneous disease among them. Indications are that this higher morbidity is stimulated by factors other than the increased transmission of pathogens from one insect to the other. It appears likely that the environmental stresses attending crowding cause metabolic changes that make the insects more susceptible to infectious agents in them or in their surroundings. This might be interpreted to the effect that it is the conditions caused by crowding that elicit the appearance of disease rather than the mere deficiency of space or room.

Under conditions of crowding, initiated at the time of hatching, deaths may occur at any time during the larval life of the insect. In some instances most of the deaths occur before the fifth instar is reached. In general, those deaths that occur in the early instars are caused by bacteria. Most of the deaths occurring in later instars are attributable to viruses. It is possible, of course, that the virus diseases in some of the insects may be activated or induced by the increased activity of the bacteria.

With some species, at least, the effects of crowding may become apparent with numbers as low as five (when restricted to a container of 13.5 cu. in.) and progressively increase as the numbers increase up until approximately 25 larvae are confined to the container. At this level, and on up, mortality reaches 100 per cent.

#### HEAT AS A STRESSOR

Our investigation as to the effects of heat on the development of disease in insects has not progressed to a point at which definite conclusions can be made. There are indications, however, that temperatures in the neighborhood of 40°C. may cause some insects (e.g., *Junonia* and *Sabulodes*) to have their body cavity invaded by bacteria more frequently than occurs in those larvae held at room temperature (22°C.). In other words, elevated temperatures appear to be conducive to a higher incidence of bacteremia than normally occurs. Presumably, this bacteremia arises from the microflora of the insect's alimentary tract. As yet, we have not observed any increase in phagocytosis in the heat-treated larvae.

Higher temperatures may also enhance the susceptibility of insects to bacteria administered intentionally. Thus, *Peridroma* which ordinarily is only slightly susceptible to *Bacillus thuringiensis* Berliner, may be markedly susceptible when held at 40°C.

Moreover, *Junonia*, *Colias*, and *Sabulodes* appear to succumb more rapidly to infection by *B. thuringiensis* when held at 40°C. than at lower temperatures.

Thus far our heat experiments have not provided any instances in which the elevated temperatures induced the appearance of virus disease.

#### CHEMICALS AS STRESSORS

So far we have found no clearcut evidence that virus is produced autochthonally or *de novo* in the insect as a result of administering chemicals of various kinds. On the other hand we have no proof that this cannot happen.

Working with *Junonia* we found that feeding the larvae hydroxylamine hydrochloride, in a manner similar to that employed by Yamafuji and associates (1952-54) did not induce the manifestation of any disease, including the virus diseases known in this insect. Nor did this chemical increase the susceptibility of *Junonia* larvae to *B. thuringiensis*. Occasionally, when larvae were fed or injected with N/3 potassium nitrite, after being held 24 hours in the refrigerator, there was a slight increase in the number of insects suffering from granulosis as compared with the control insects. No increase in disease incidence has been noted in experiments in which sodium fluoride, peroxide, or ether were used as stress chemicals.

In our experiments using *Peridroma* larvae as the test insects, the administration of hydroxylamine hydrochloride did not induce either the polyhedrosis virus or the granulosis virus known in this insect. Nor did it increase the insect's susceptibility to *B. thuringiensis*. We have conducted a large number and variety of experiments in which different concentrations of potassium nitrite (alone or in combination with refrigeration, in the manner used by Yamafuji with silkworms) were fed to *Peridroma* larvae. In general, the test insects showed an increased mortality up to three times that occurring in the controls. In one experiment, a slightly higher percentage of the test insects, than the controls, died from polyhedrosis virus and from microsporidian infection. Most of the deaths, however, in this and all other experiments appeared to be caused by bacteria which presumably invaded the body cavity from the alimentary tract of the chemically damaged or weakened insect. In some cases, the increase of bacterial disease in the test insects, over the controls, was very pronounced. It was also found that the administration of N/10 sodium fluoride, especially when injected into the body cavity of *Peridroma* larvae, also caused an increase in the occurrence of bacterial infection. To what extent, however, this is a result of the invasion of chemically injured tissue by bacteria we are not prepared to say.

We have performed a number of experiments with chemical stressors using the silkworm as a test animal. In no case were we able to duplicate the results reported by Yamafuji using potassium nitrite or hydroxylamine sulfate. Sometimes, in these experiments, we obtained mortalities of from 75 to 100 per cent, but not a single death could be attributed to the presence of a virus. (We attributed the deaths to poisoning by the test chemical, or to intercurrent infection by bacteria.) It should be pointed out, however, that the strain of silkworm used in our experiments was the Hungarian strain received from Dr. G. H. Bergold, and which Dr. K. Yamafuji found somewhat resistant to his virus induction methods. Moreover, we have not, as yet, observed any results that may appear in succeeding generations of chemically treated caterpillars. Using this same strain of silkworm, we have not been able to elicit virus by treatment of the insects with sodium fluoride, as did Veneroso (1934) and Vago (1951) using other strains of silkworm.

Incidentally, early in the course of our experiments on the role of stress in the diseases of insects we sought to ensure healthy stocks of larvae by disinfecting the eggs by immersing them for 1½ hours in 10 per cent formaldehyde, followed by a 15 minute aqueous rinse. While this treatment may have disinfected the eggs, we have found considerable evidence indicating that it also caused the larvae from such eggs to be more prone to disease than larvae from untreated eggs. As yet, we are not in a position to explain this phenomenon, but it would appear to be the outcome of a stress exerted by the chemical.



It might be mentioned here that subsequent to similar experiments by Briggs in our laboratory, we ran a number of cursory tests to determine if the injection of zymosan would permit the activation of latent virus or bacteria in *Junonia*, *Colias*, *Peridroma*, and *Estigmene*. (Zymosan is an insoluble carbohydrate complex derived from yeast cell walls, and combines with properdin in vertebrate serum.) The results with regard to the activation of latent virus were inconclusive. Also, in *Colias*, it was observed that whereas there was approximately a 38 per cent mortality in the case of larvae injected only with the bacterium *Escherichia coli* (Migula), in larvae injected with both *E. coli* and zymosan the mortality was about 70 per cent. Similar results were obtained when *Peridroma* was used as the test insect. In the latter insect, when *B. thuringiensis* was used as a test organism it alone caused virtually no deaths, whereas when it was fed to insects concurrently with the injection of zymosan, up to 68 per cent of the larvae died from infection with the bacillus.

#### OTHER STRESSORS

We have not had the opportunity to proceed very far in our investigation of the effects of other stressors in relation to disease in insects.

Early in 1956, Dr. J. Weiser informed us of experiments he was conducting on the effects of triturated glass in certain bacterial infections in silkworms. He found that the ingestion of such glass by the caterpillars caused them to become more susceptible to attack by certain ingested bacteria. We have included triturated glass in our experiments relating to the effect of abrasives in infections in insects. In general, triturated glass alone fed to *Junonia*, *Colias*, *Sabulodes*, and *Bombyx*, along with their food or by microfeeder, induced no appreciable amount of disease in larvae of these insects. In one experiment in which glass was fed continuously to silkworm larvae together with a strain (0-8-13) of *Serratia marcescens* Bizio, the mortality amounted to approximately 70 per cent as compared to 20 per cent when *S. marcescens* alone was fed, and 0 per cent when triturated glass alone was fed.

Our studies on the role of nutrition in insect diseases have been of a preliminary nature only. Because of Vago's (1951) finding that 70 per cent of the silkworms fed on leaves of *Maclura aurantiaca* Nutt. succumbed to a polyhedrosis we have conducted a similar experiment using the foliage of *Maclura pomifera* (Raf.) (Osage orange). Using the Hungarian strain of silkworm that we had originally received from Bergold, we fed 125 caterpillars exclusively on leaves of *Maclura* throughout their larval lives. Not a single case of polyhedrosis appeared. The larvae were allowed to pupate, the adult laid eggs from which, at the present writing, we hope to obtain a second generation of larvae which will be observed for the presence of polyhedrosis virus. This experiment, as have others, indicates that the particular strain of silkworm used in our investigation carries little, if any, latent virus.

Using a General Electric 15 watt germicidal lamp (2537Å), we have so far found no indication that exposures to ultraviolet light increases the susceptibility of *Junonia* larvae or of silkworms to *B. thuringiensis*. Nor has there been any increase, as the result of such exposures, to the amount of spontaneous infection, either virus or bacterial, occurring in these species. In the case of *Peridroma* larvae, however, exposures, for various periods, have caused mortalities of from 75 to 100 per cent in which bacteria from the insect gut appear to be primarily involved. The incidence of virus infection in the test insects was no higher than in control larvae.

It may be said that while our work has not progressed to a point where we can draw final conclusions, we have obtained results which indicate that microorganisms present in a latent state in the tissues of an insect host can be activated by the influence of certain incitants, that stress may so weaken or condition an insect as to make it susceptible to microorganisms ordinarily not pathogenic to it, and that stress may cause an insect to be more susceptible to a known pathogen than it is ordinarily. On the other hand, the provocation of disease by stress may not be as uniform or as regular, by our experimental methods or in nature, as has been indicated by some authors. We hope soon to be able to present data in a more concrete form to support these generalizations.

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# Role of Deoxyribonucleic Acid and Deoxyribonuclease in Induction Processes of Polyhedrosis Virus

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## ABSTRACT

*The finding that hydroxylamine can provoke a virus production in silkworms was made in 1943. Systematic study on chemical induction of polyhedrosis has been conducted since then.*

*Hydroxylamine is formed by reduction of nitrites and gives oximes after combining with ketones. We found further that polyhedral virus is produced by potassium nitrite or acetoxime.*

*These inducers inhibit catalase in tissues; the virugenic action was also demonstrated for hydrogen peroxide. All inductors thus appear as intermediates of larval metabolism; another confirmation for this was obtained by the discovery of two new enzymes, named oximase and transoximase.*

*It was observed that four kinds of virugens depolymerize deoxyribonucleic acid directly or indirectly, and that they activate deoxyribonuclease in cells. The depolymerization may be the first step of viral formation.*

*An activation of cellular proteases is caused by inducing reagents, too. In addition, DNase and trypsin have the ability to produce jaundice. Proteolysis would be a preliminary reaction for virugenes.*

*Deoxyribonucleic acid was isolated from healthy worms and freed from ribonuclease as well as protein. We confirmed that the purified DNA possesses a polyhedrosis-inducing function. The virugenic activity of deoxyribonuclease was elevated by deoxyribonuclease or trypsin.*

*The demonstration that polyhedrosis is induced by DNase-digest of nuclear DNA was achieved recently. Previral substances must be relatively small components in large molecules or aggregates of deoxyribonucleic acid in the nucleus. Discussion on internal or external origin polyhedral virus is losing its significance.*

## INTRODUCTION

In 1931, I began biochemical studies on silkworms, and in the early stage, properties of various enzymes were investigated particularly in connection with physiological conditions (1). These were the first quantitative investigations on the enzymatic action in insects, and ten years' experience has led me to the assumption that polyhedrosis might be provoked without viral infection.

The initial hypothesis was that polyhedra would be formed by specific abnormal metabolic reactions in cells. It was thus assumed that a disorder in the nucleoprotein metabolism is the principal process in the jaundice production, and that hydrogen peroxide may be one of the agents which cause such a disturbance. In the first period, therefore, we studied mainly the relation between respiration and catalase in virus-diseased tissues of several plants and animals. It was observed that the development of viroses brings about a respiratory deviation which leads to an accumulation of hydrogen peroxide, and that the peroxide treatment occasions a denaturation of proteins in organisms. We were, however, unable to produce viral particles artificially by hydrogen peroxide. Consequently, I sought reagents which retard the decomposition of the peroxide in hosts, and discovered the special function of hydroxylamine. When larvae of *Bombyx mori* were appropriately fed with the amine, the catalytic activity of them was greatly hindered without appreciable lowering of oxygen inhalation and a virus formation was induced in their nuclei. We found further that barium peroxide has the ability to provoke polyhedrosis, and that the multiplication of some viruses is prevented to a certain extent by iron compounds. The results mentioned above were summarized in 1949 (2).

It seemed desirable to demonstrate that jaundice inducers are metabolites. We confirmed actually that the oxime content of a larval body increases after feeding with nitrates, nitrites, hydroxylamine or ammonium salts, and that the viral induction is also caused by acetoxime as well as by potassium or sodium nitrite. In these tests, the inductors were usually administered under virus-sterilized conditions. The chemical virugensis was also successful for a foreign stock sent from Canada. Generally, N/3-1 N solutions of reagents were given at the first meal time in the fourth instar, and thereafter the administration was performed once each day, after a hunger period of several hours. Sometimes, accessory means were applied to stronger strains; in most cases, worm bodies were cooled at 1-3 °C for 10-24 hours. It was verified that virogenic treatments provoke an activation of proteases in tissues. On the other hand, the existence of nitrate reductase was proved in this animal, and a new enzyme, called oximase, was discovered which catalyzes the conversion of oximes into amino compounds. There is, accordingly, the possibility that insects can assimilate inorganic nitrogen. Furthermore, we ascertained that nitrite or acetoxime too inhibits cellular catalase. It appeared then necessary to examine whether any difference exists between the property of artificially produced polyhedra and that of naturally occurring ones. Examinations showed that the chemical polyhedron has a lower solubility, weaker infectivity and looser structure than the natural one. We supposed further that incipient virugenic reactions happen inside of the nucleus. It was established that the enlargement of nuclei, aggregation of chromatins as well as anomalous nuclear division are brought about by feeding with chemicals. In view of these findings, I surmised that polyhedral virus may originate from genes in somatic cells. The experimental results obtained in this second stage were reviewed in 1952 (3).

#### INDUCTION AND INFECTION

At that time, there was still a suspicion that induced polyhedrosis might be due to the provocation of the reproduction of infected viral particles. We conducted some additional experiments about the problem. Larvae or pupae of *Bombyx mori* were inoculated with a polyhedral solution and the inductive procedure was applied to their descendants as well as to the offspring of uninfected worms. The numbers of jaundiced individuals in both groups were almost the same (4). A presumption was also made that chemical treatments would give occasion for producing any immature form of virus which could be transmitted to the progeny. We treated caterpillars with an inducing reagent and fed their progeny again with the inducers. There was no acceleration of virosis development (5). It is conceived that a viral precursor occurs in embryos as a kind of normal constituent. Eggs were immersed in solutions of virogens and emerged larvae reared in the usual way. Some of them were attacked by polyhedrosis (6). We must then presuppose that previrus is present in chromosomes. If so, it is expected that the virus formation may be promoted by the interspecific hybridization. *Bombyx mandarina* was crossed with *B. mori* and the hybrid bred under unfavourable circumstances. Jaundice developed in numerous worms in the F<sub>2</sub>-generation (7).

In order to produce viral particles chemically, it is essential to let larvae take a fairly large quantity of reagents. The feeding method, however, is not always applicable, because some stocks dislike to eat them. Therefore, an injection process was devised; in general, solutions of N/10-N/5 KNO<sub>2</sub> or NH<sub>2</sub>OH were injected every day into fourth instar caterpillars. We recognized that the procedure is not so effective, but that the virugensis can be accelerated by the crossing of different strains or long refrigeration of eggs (8). As described in the foregoing chapter, I conjectured the virogenic potency of hydrogen peroxide more than fifteen years ago. Many papers concerning the behaviour of peroxide in living cells were published from our institute (9). In the meanwhile, Ishimori and Osawa in Tokyo carried out a series of experiments certifying my theory and succeeded in producing polyhedra after treating with H<sub>2</sub>O<sub>2</sub> (10).

During the induction tests, we noticed often that the insect contracts jaundice in touching chemicals. The resistance of the larval body to inductor solutions was now studied and a peculiar observation obtained that silkworms are able to live in 5-15 N hydrogen peroxide for 3-15 minutes (11). Subsequently, we elaborated a contact



method; caterpillars immediately after the second or third ecdysis are first dipped entirely into N/10-N/5  $\text{NH}_2\text{OH}$  or N/6-N/3  $\text{H}_2\text{O}_2$  for 3-5 minutes and then kept in the state of half immersion for 20-100 minutes. The time of soaking and concentration of the agent must be varied according to the physical strength of the animal. The treatment lasts several days (12). Polyhedrosis was also induced by steeping in thioglycolic acid which Lwoff and Siminovitch employed for the bacteriophage production (13).

### OXIMASE AND TRANSOXIMASE

One of the characteristic points in polyhedral virogenesis is that inducers can be easily transformed in host cells. The discovery of oximase in the silkworm is evidence of this. Moreover, it was testified that the content of oxime and oximase is higher in viroosed larvae than in healthy ones (14). In those experiments, the enzymic action was estimated by measuring the volume of amino-N converted. Later, the determination of the enzyme was performed colorimetrically, by estimating the decrease of pyruvic oxime (15). Recently, we improved the procedure in which glucosoxime was used as substrate (16).

In the course of pursuing the variation of hydroxylamine derivatives in tissues, I perceived that the oxime group is spontaneously transferred to another carbonyl compound, and that the transference can be promoted by an enzyme denominated transoximase (17, 18). The enzymatic power increases after viral inoculation (19). At the beginning, the estimation of the enzyme was carried out by distilling a mixture of acetaldehyde oxime and acetoxime produced from pyruvic oxime (20). A chromatographic process was then introduced for the measurement of enzymic transoximation (21, 22). Recently, we determined the transoximase by conveying the oximino radical from glucosoxime to pyruvic acid. (23).

The confirmation was made that the activity of oximase and transoximase is elevated after administering virogens (24, 25, 26, 27). These enzymes were demonstrated in other organisms, too; this suggests, however, that the reduction and conversion of oximes have connection with proteinous metabolism (28, 29, 30, 31). Nitrogen in oximino or protein must come partly from nitrates in food. In our laboratory, Omura investigated the specificity of silkworm nitrataase and found that this enzyme competes with oximase for hydrogen donators (32, 33, 34).

Polyhedral virus is enveloped in a great amount of protein. A proteolysis should take place before viral multiplication. It seems necessary that surrounding proteinous substances are decomposed prior to the maturation of previrus in the nucleus. Yoshihara continued her protease study and reported that the hydrolysis of peptide or pepton in larval tissues is strengthened after infecting with polyhedra or inducing with chemicals (35, 36, 37, 38, 39).

### INDUCER AND DEOXYRIBONUCLEASE

It is well known that ribonucleic acid has some influence upon the synthesis of proteins. In *B. mori*, the content of the acid was not so considerably affected by inductive treatment or viral infection (40, 41). We observed afterwards that the virus-producing agents activate ribonuclease in the body, and inferred that the fragments of RNA relate more closely to the protein formation (42). Eto of this institute indicated that the silkworm nucleus contains ribonucleate abundantly, and that the percentage of adenine in the acid is pretty low (43, 44).

The disintegration of other carbohydrates than ribose concerns chiefly the supply of energy. We substantiated that the application of virogenic reagents causes the activation of amylase and invertase in caterpillars (45). From his induction experiments with fluoride, Vago deduced an intimate relationship between polyhedrosis production and glycolysis reaction (46).

Jaundice virus, however, is a deoxyribonucleoprotein. It appears, therefore, reasonable to presume that virugens attack DNA. We could attest that inducing agents, especially hydrogen peroxide, disintegrate deoxyribonucleate (47). It was further observed that the action of DNase in the gut, blood or tissues is augmented after treating with inductors, but that the enzyme in the digestive juice is impeded by severe treatment (48). Subsequent researches showed that the increment of nucleases as well as



of proteases occurs soon after injecting virus or inducers (49). The result taught me that there is a probability of producing polyhedrosis by strong enzymes. We were thus able to corroborate that the injection of crystalline pancreatic deoxyribonuclease or trypsin brings about the viral formation (50).

### VIROGENESIS AND DNA

The reproductive principle in the polyhedron is deoxyribonucleic acid. Previrus component should be DNA in the cell. Nuclei were isolated from normal silkworms and DNA-fraction was prepared from them. Virosis developed in individuals injected with an alkaline solution of the nucleic acid (51, 52).

It is uncertain, however, whether previral deoxyribonucleic acid can start reproduction without cooperation of cellular proteins. The form of polyhedral precursor was repeatedly discussed and some supplementary investigations were carried out in relation to this (53, 54, 55, 56). Caterpillars were infected with virus or administered with chemicals and then injected with isotopic phosphorus. The proportion of  $P^{32}$  incorporated into polyhedra in relation to the phosphorus introduced into bodies was very small. It is supposed that the viral formation may be only one course of deviated metabolic processes (57, 58). Lately, the injection of  $P^{32}$ -polyhedron was performed and the P-content of newly produced polyhedral crystals estimated. A similar experiment was simultaneously conducted using inactivated  $P^{32}$ -virus and untreated viral solution. We confirmed that the ratio of the phosphorus transmitted to the virus progenies is under 0.5% in both cases. It can be concluded that most of polyhedral nucleic acid is decomposed in host tissues (59). On the basis of their examination into chromatic masses, Smith and Xeros drew the inference that polyhedrosis virus behaves rather like a differentiated product of altered cell metabolism (60).

It might be possible that descendants from infected parents would be resistant to original viral particles. A polyhedral solution was injected into worms and the progeny in the fourth to eighth generation were inoculated with the same virus preparation. The data showed, however, that the susceptibility to jaundice is not lowered by the previous infection (61). It was also observed that the neutralizing capacity of immunized serum is weak (62). Furthermore, larvae of another group were violently treated with virogens for four generations and the greater part of them killed intentionally. We proved that the resistance to inductors is not increased by such treatments. The deduction that previral substances must be ingredients proper to cellular function has thus been supported (63).

The polyhedral formation proceeds principally in the nucleus. After verifying the occurrence of an eclipse period in the jaundice disease, we further demonstrated that insect nuclei in this stage can produce some factors which have the faculty to accelerate the viral multiplication (64, 65). The activity of hydrolases and nucleases in the host body was really raised by injecting a nuclear mass (66). Besides, the nucleus contains a considerable quantity of uric acid; this is an indication of intensive catabolism of nucleates in it (67).

Intense enzymic decomposition of deoxyribonucleic acid in cells would take place after removal of circumferential proteinous constituents by activated proteinases. A special portion in degraded DNA-molecules should act as previrus. The worm nucleic acid freed from ribonucleate as well as protein was disintegrated with pancreas deoxyribonuclease crystals. We proved that the digest possesses a virosis-inducing power (68).

The depolymerization of DNA discloses probably new configurations and the resultant small units must regulate synthetic rearrangements of distinctive proteins. A survey by Eto revealed that polyhedra dissolve specifically in acidified alcohol (69, 70). Morgan, Bergold, Moore and Rose illustrated the viral particles enclosed in a macromolecular, paracrystalline lattice (71). We too published reports describing that electrophoretic and ultracentrifugal patterns of chemically produced polyhedral protein are slightly different from those of naturally prevailing ones (72, 73, 74, 75). Mechanism of polyhedron formation has thus many peculiarities and the speculation was also made that the virus could be derived from the deoxyribonuclease-controlling gene (76, 77, 78, 79, 80). We substantiated actually that the DNase content of polyhedral crystals is nearly twenty times as much as that of larval cells (81).

## CONCLUSION

Deoxyribonucleic acid may be previrus for polyhedrosis. In chemical virogenesis, DNA-depolymerization should be one of the principal reactions and proteolysis would be a preliminary step.

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#### DISCUSSION

N. PLUS (MRS.). Is it possible to have one strain of *Bombyx mori* with no spontaneous polyhedrosis?

K. YAMAFUJI. We have special strains which have bred under virus-sterilized conditions for many generations. Even in these stocks there are a few polyhedrosed individuals in mid summer. No diseased larvae appear spontaneously in spring or autumn.

# Latente und akute Infektionen mit Insekten-Viren

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## ZUSAMMENFASSUNG

Auf Grund von Untersuchungen über die Polyedrose von *Neodiprion sertifer* wird die Bedeutung der latenten Verseuchung von Populationen für die Epizootologie dieser Krankheit und für Insektenvirosen im allgemeinen diskutiert. Die Manifestation latent vorhandener Infektionen wird als ein Ausgangspunkt für Virusseuchen angesehen. Ist die Krankheit in ihr akutes Stadium getreten, so wird sie durch Kontakt seuchenhaft auch auf gesunde Individuen und Stämme weiter verbreitet. Ablauf und Ausgang der Seuche ist durch die Toleranz des Wirtes bedingt und führt günstigenfalls zur Zurückdrängung der Virose in ihr latentes Stadium. Durch Verdünnung des latent "vererbten" Pathogens über Generationen ist der Übergang latent verseuchter Stämme in gesunde denkbar. Die Ansicht von Yamafuji über eine "artificial virus formation" zur Erklärung der Genese von Insekten-Virosen wird abgelehnt. Eigene Versuche an *Bombyx mori* zu diesem Problem werden besprochen.

Im Gegensatz zur Pathologie, die sich die Aufgabe stellt, die Pathogenese, d.h. das Zustandekommen der Einzel-Erkrankung zu erhellen, versucht die Epizootologie (syn. Epidemiologie) die Bedingungen zu erforschen, die zu Massen-Erkrankungen in Populationen führen. Für die epizootologische Forschung sind daher besonders die Ergebnisse der Populationsdynamik von grundlegender Bedeutung.

Nicht alle Infektionskrankheiten können als seuchenhafte Erkrankungen bezeichnet werden. Unter Seuchen versteht man speziell solche Infektionen, bei denen sich der Erreger fast ausschliesslich im Makroorganismus vermehrt, bei denen sich also das Geschehen von Tier zu Tier direkt oder indirekt überträgt und sich so aus eigenem Bestand erhält. Zu ihnen gehören daher mit Vorrang die Viruserkrankungen.

Wichtige Probleme der Epizootologie sind das Auftreten von Seuchen, der Ablauf derselben, ihre Weiterverbreitung und ihr Verlöschen. Diese Fragen sind eng mit der Pathogenese der zur Diskussion stehenden Erkrankung verknüpft und sollen hier speziell im Hinblick auf Viruserkrankungen von Insekten diskutiert werden.

Der Verlauf einer Seuche ist einmal abhängig von der Virulenz des Erregers und seinen Ausbreitungsmöglichkeiten. Ein gleichwichtiger Faktor ist die Empfänglichkeit (Disposition) oder anders ausgedrückt die angeborene Immunität (*immunité naturelle*) bzw. die Resistenz des Wirtes gegenüber der Infektion. Durch eigene Beobachtungen und einschlägige Untersuchungen an den von uns untersuchten Insekten-Virosen von *Neodiprion sertifer* (Kernpolyedrose des Mitteldarms), *Bombyx mori* und *Aporia crataegi* (Kernpolyedrose mesenchymaler Gewebe), *Dasychira pudibunda* (Plasma-polyedrose des Mitteldarms) konnten bisher keine Beweise dafür erbracht werden, dass es bei Insekten eine (individuell) erworbene Immunität (*immunité acquise*) gibt. Wir sind daher geneigt anzunehmen, dass eine solche nicht existiert.

Was nun den Ausbruch von Virus-Seuchen bei Insekten betrifft, so kann dieser durch Einbruch von Erregern in eine Population erfolgen oder durch Manifestation der Krankheit in einer bereits latent verseuchten Population. Für beide Fälle kennen wir Beispiele. Die folgenden Ausführungen beschränken sich auf die von uns untersuchten Verhältnisse bei *Neodiprion sertifer* und *Bombyx mori*.

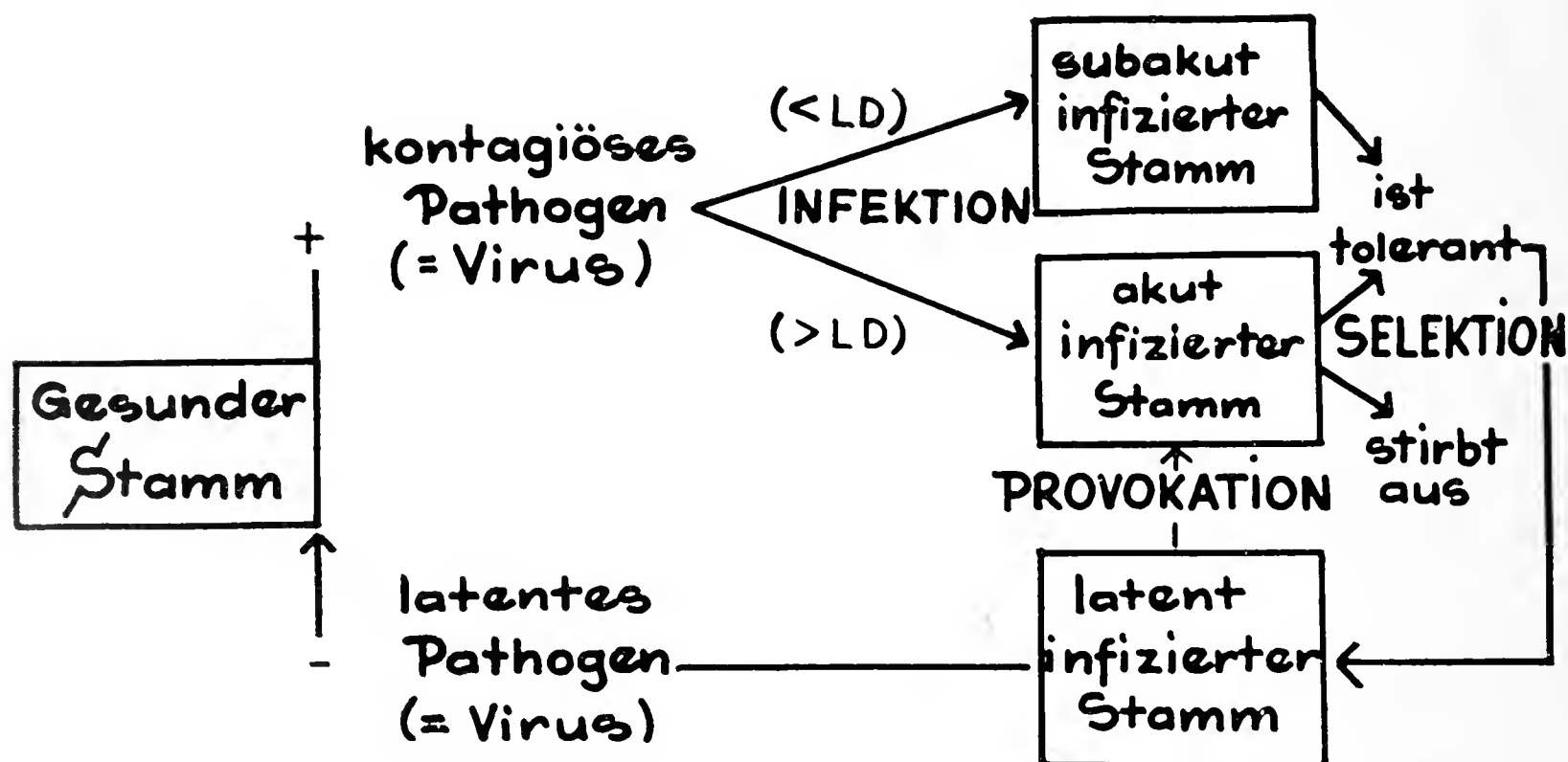
Die Blattwespe *Neodiprion sertifer*, zur paläarktischen Fauna gehörig, war in Nordamerika nicht heimisch. Sie wurde erst in unserem Jahrhundert dort eingeschleppt, wo sie sich rasch vermehrte, da hier ihre wesentlichen natürlichen Feinde fehlten. Zu den biotischen Begrenzungsfaktoren gehört in Europa u.a. eine Virus-Seuche. Bis zu Beginn der 2. Hälfte unseres Jahrhunderts blieben die nordamerikanischen Populationen gesund; das Auftreten der spezifischen Polyeder-Virose konnte nie beobachtet werden. Damals importierte Bird die Viren aus Europa und es gelang ihm, mit ihnen gesunde Populationen von *N. sertifer* in Kanada künstlich zu infizieren. Mit Hilfe der künstlichen Verbreitung der Virus-Seuche konnte eine wirksame biolo-

gische Schädlingsbekämpfung durchgeführt werden (Bird 1953). Etwas anders liegen die Verhältnisse in Europa, wo die Seuche enzootisch (syn. endemisch) auftritt. Die Virose bringt hier Gradationen dieses Forstschädling im allgemeinen, wenn auch immer erst sehr spät, zum Zusammenbruch. Durch künstliche Applikation von Polyeder-Virus gelingt es jedoch, wie Franz und Niklas (1954) zeigen konnten, den seuchenhaften Zusammenbruch durch eine Superinfektion vorzuverlegen.

Im Folgenden sollen Beobachtungen in Zusammenhang mit dem enzootischen Auftreten der Polyeder-Seuche von *N. sertifer* in Europa diskutiert werden. Das wiederholt spontane Auftreten der Virose in anscheinend gesunden Populationen von *N. sertifer* in der Dähe von Darmstadt (vgl. Krieg 1955a) liess auf eine inapparente Infektion der Stämme des Enzootie-Gebietes schliessen. Zur Klärung dieser Frage wurden eingehende Untersuchungen angestellt, über die hier kurz berichtet werden soll (Krieg 1956).

Zur Untersuchung gelangten 3 Stämme von *N. sertifer*, mit A, B und C bezeichnet. Bei der Population A waren die Imagines aus gesunden Laborzuchten des Vorjahres (Vergleichszuchten) hervorgegangen und wurden an bisher von Blattwespen nicht befallenen Kiefernäzweigen zur Eiablage eingebeutelt. Die Population B wurde aus einem Befallsgebiet von *N. sertifer* bei Darmstadt, Süd-Westdeutschland, die Population C aus einem Befallsgebiet bei Ülzen, Nord-Westdeutschland, entnommen. Die Versuche hatten das Ziel, mit Hilfe verschiedener Provokationsmittel die latent vorhandene Virose zum Ausbruch zu bringen. Es wurden neben Bestrahlung auch Chemikalien appliziert. Als wirksam erwies sich: UV-Bestrahlung, Thioglykolsäure, Natriumfluorid und Hydroxylamin. Die verwendeten Populationen zeigten verschiedenes Verhalten: Die unter besonderen Kautelen herangezöchtete Population A reagierte auf keines der Mittel. Dagegen konnte in den beiden aus dem Freiland des Endemiegebietes entnommenen Populationen B und C reproduzierbar eine Polyedrose induziert werden. Die Ergebnisse werden dahingehend interpretiert, dass die Freilandpopulationen des Enzootiegebietes im Gegensatz zur Population A latent infiziert waren.

Ob nun eine Virose in Form einer akuten Infektionskrankheit verläuft und in deren Folge zur Vernichtung einer Population föhrt oder nicht, ist vom Gleichgewichtszustand zwischen Erreger und Wirt abhängig. Die Verhältnisse lassen sich vielleicht am besten mit Hilfe eines Schemas zum Ausdruck bringen (Schema I). Hier sind die Möglichkeiten aufgezeigt, die zu einer Epizootie föhren können: In eine gesunde, aber sensitive Population wird der spezifische Krankheitserreger eingeschleppt,



Schema 1:

(Virus = const.  
Wirt = var.)



und es kommt damit zu einer akuten Infektion des Stammes. In diesem akuten Stadium, das durch starke Vermehrung des Erregers im Wirtstier ausgezeichnet ist, verbreitet sich die Krankheit über Infektketten von Tier zu Tier und vermag so die örtliche Population zu vernichten, wenn der Stamm genügend sensitiv, das Virus hochvirulent ist und die Ausbreitung schnell vor sich geht. Sind diese Bedingungen nicht erfüllt, so toleriert ein Teil der Wirtspopulation den Erreger. Beispielsweise tolerierte die latent verseuchte Population B das latente Virus bis 24%. Nach Provokation mit NaF sank die Toleranz bis auf 0%. Den gleichen Erfolg hatte Superinfektion. Nach künstlichen Infektionsversuchen an einer gesunden Population A tolerierten 7,6% der Tiere das kontagiöse Virus, die übrigen starben an der Folge der experimentellen Virus-Infektion. Die Tiere, welche die Seuche tolerierten, waren, wie die Untersuchung ergab, nicht etwa gesund, sondern latent verseucht. Andererseits kann eine latente Verseuchung auch dadurch entstehen, dass der Wirt mit einer ungenügenden Dosis infiziert wird. Die  $LD_{50}$  (= Dosis, bei der 50% der Tiere absterben) wurde von uns überschlagsmässig zu 50 — 100 Polyeder bestimmt. — Im latenten Zustand wird das Virus wohl nicht mehr durch zufällige Infektketten jenseits eines Zeugungszusammenhangs übertragen, sondern nach Erfahrungen von Roegner-Aust (1949), Clark (1955), Bird (1955) und anderen Autoren germinativ, d.h. es wird gleichsam "vererbt".

Wie schon erwähnt, gelingt es, in latent verseuchten Stämmen durch bestimmte Mittel (neben den schon genannten auch Futterwechsel) die Seuche zu provozieren. Indem auf diese Weise die Disposition des Wirtes gesteigert wird, verschiebt sich das Gleichgewicht zu Gunsten des Erregers und die Krankheit tritt wieder in ihr akutes Stadium.

Durch Selektion können aus latent verseuchten Populationen im Laufe von Generationen auch wieder gesunde Stämme hervorgehen. Vago (1953) gelang es, durch eugenische Massnahmen (Anwendung von Provokationsmitteln) aus latent verseuchten Zuchten von *Bombyx mori* wieder einen hohen Prozentsatz gesunder Individuen herauszuzüchten.

Auch der umgekehrte Vorgang, nämlich die Anreicherung von Virusmaterial im Verlauf von Generationen ist eine oft zu beobachtende Erscheinung und zwar als Begleiterscheinung von Retrogradationen des Wirtes. Ein Beispiel hierfür lieferten Beobachtungen an Individuen aus aufeinanderfolgenden Generationen von *N. sertifer*, die aus dem Enzootiegebiet stammen: Während in der P-Generation (B), die Spontanmanifestationen um 20% lagen, stiegen sie in der F-Generation (B') auf über 70% an.

Ob die genannten Ursachen die einzigen sind, die für den Ausbruch und die Verlaufsform einer Epizootie in Frage kommen, ist noch fraglich. Auch selektionsbedingte Steigerung der Virulenz durch geeignete Wirtspassagen innerhalb der Infektkette bzw. Abschwächung der Virulenz könnten wirksam sein. So sieht z.B. Cox (1954) schliessliche Funktion der Virus-Variabilität an.

Beispiele für Variationen bei Insektenviren fehlen bisher.

Offenbar sind latent verseuchte tolerante Populationen die Voraussetzung für ein enzootisches Auftreten von Virose. Eine Epizootie dagegen hat den Einbruch kontagiöser Erreger (aus einem Virus-Reservoir) in eine empfindliche Population zur Voraussetzung. Praktisch kommen diese beiden Extreme oft gemischt vor, indem in einem Enzootie-Gebiet durch Super-Infektion eine Art epizootische Welle auftritt. Der Infektionsversuch von Franz und Niklas (1954) in Freiland dürfte hierfür ein Modell sein.

Damit sind zusammenfassend einige wichtige Punkte epizootologischer Forschung berührt worden, soweit sie aus Beobachtungen an Insektenvirose ableitbar sind. Abschliessend soll noch das "neue" Auftreten von Virusseuchen etwas näher betrachtet werden.

Da die Viren fähig sind, mit dem Kernmaterial der befallenen Zellen um Wirkungsmöglichkeit zu konkurrieren, hat man es nicht an Versuchen fehlen lassen,

Viren mit freigewordenen — quasi asozialen — Wirtsgenen zu identifizieren. Insbesondere Yamafuji (1950 und 1952) berichtete über eine "artificial virus formation" bei *Bombyx mori*.

Als Beweis für seine These führte Yamafuji Versuche an, in deren Verlauf es ihm gelungen sein soll, in gesunden Zuchten von Seidenraupen mit Hilfe bestimmter Chemikalien eine Polyeder-Virose zu induzieren. Vago (1953), der ähnliche Versuche durchführte, deutete seine Ergebnisse als Provokation einer latenten Virose. Die Klärung der Streitfrage (künstliche Virusgenese oder Provokation latenter Virose) war lediglich durch einen negativ ausfallenden Induktionsversuch an nicht nur symptomatisch, sondern wirklich gesunden Populationen im Sinne von Vago zu entscheiden. Glücklicherweise gelang uns Beschaffung und Aufzucht eines wirklich gesunden *B. mori*-Stammes, mit dem die einschlägigen Induktionsversuche durchgeführt werden konnten. (Krieg 1955b). Keines der Versuchstiere starb hierbei an der Virose; der benutzte Stamm war also wirklich gesund. Auch die im folgenden Jahr durchgeführten Provokationsversuche an der F-Generation fielen wiederum negativ aus. Die Ergebnisse von Yamafuji lassen sich somit nur als Provokation der spezifischen Polyedervirose in latent verseuchten Stämmen im Sinne von Vago verstehen. Steinhaus (1955) kam unabhängig von uns zu den gleichen Ergebnissen. Die Theorie von Pasteur (1860), wonach es keine permanente "generatio spontanea" gibt, konnte jedenfalls im Bereich der Insekten-Viren durch die bisherigen Befunde von Yamafuji nicht entkräftet werden.

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# Le Virus non pathogène de la Drosophile, son Intégration au Système génétique de la Mouche

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## RESUME

*Deux types de relation peuvent exister entre le même virus et les mêmes cellules-hôtes: un équilibre symbiotique que l'on peut appeler "latence" ou bien un cycle infectieux typique d'une multiplication virale.*

Le virus de la Drosophile, ou virus  $\sigma$ , a été extensivement étudié depuis 10 ans et une revue de l'ensemble de ses propriétés a été publiée en 1954 par L'Héritier. Dans le cadre de ces exposés sur la latence des virus d'Insectes, je ne discuterai ici que des deux modes de relation fort différents qui peuvent être réalisés entre le même virus et les mêmes cellules-hôtes. Les faits expérimentaux correspondants, ainsi qu'une discussion plus approfondie, sont exposés aux références suivantes: Plus (1954 et 1950), Brun et Sigot (1955), Brun (en préparation).

Le virus de la Drosophile n'est jamais pathogène dans les conditions biologiques normales et il n'est pas non plus contagieux. Il est cependant très facile à déceler au Laboratoire. En effet, les Drosophiles qui l'hébergent, ou Drosophiles sensibles, sont tuées par une courte exposition au  $\text{CO}_2$ , alors que les Drosophiles normales, ou résistantes, sont simplement narcosées.

Ce virus est normalement transmis par hérédité, indépendamment des gènes chromosomiques. Il peut être également transmis par inoculation artificielle.

C'est l'étude des modalités de la transmission héréditaire qui nous a permis de distinguer deux catégories de Drosophiles sensibles que nous appelons les Drosophiles stabilisées et les Drosophiles non stabilisées.

**PROPRIÉTÉS DES DROSOPHILES NON STABILISÉES:** Les femelles de cette catégorie ne transmettent le virus qu'à une partie de leurs descendants, et ceci, pendant une partie de leur période de ponte.

Les mâles correspondants, eux, ne transmettent pas du tout la sensibilité. Chez ces Mouches non stabilisées, par ailleurs, la cinétique de la multiplication du virus est typique des infections virales. Elle aboutit à un rendement élevé en virus.

**PROPRIÉTÉS DES DROSOPHILES STABILISÉES:** Les femelles de cette catégorie transmettent la sensibilité à tous leurs descendants, et ceci, pendant toute leur période de ponte. Les mâles stabilisés transmettent partiellement.

Ces Mouches, de plus, présentent toujours un rendement final en virus nettement inférieur à celui des Drosophiles non stabilisées. Le taux de multiplication est également plus faible.

Nous savons que les différences entre ces deux catégories de Drosophiles ne correspondent ni à la sélection d'un génotype particulier de Drosophile ni à la sélection d'une forme mutante du virus.

Elles ne correspondent pas non plus aux deux modes possibles d'acquisition de la sensibilité: apport par les gamètes ou inoculation artificielle. Parmi les Mouches non stabilisées se rencontrent, par exemple, aussi bien les Mouches inoculées que celles héritant la sensibilité de leur père.

**PASSAGE DE L'ÉTAT STABILISÉ À L'ÉTAT NON STABILISÉ:** Les souches stabilisées sont stables par hérédité maternelle. Les femelles stabilisées n'ont, en effet, que des filles stabilisées.

Il n'en est pas de même des souches non stabilisées.

Les filles sensibles des femelles non stabilisées sont, pour la plupart, des non stabilisées, mais certaines d'entre elles sont stabilisées. De telles femelles stabilisées continueront à apparaître, ainsi, à chaque génération, parmi les filles des non stabilisées.

La stabilisation apparaît, donc, comme un événement génétique irréversible qui a les caractères d'une véritable mutation.

**HYPOTHÈSE DE L'INTÉGRATION:** Nous avons vu que les Mouches stabilisées qui sont les plus pauvres en virus infectieux sont celles qui transmettent le mieux le virus à leur descendance. Nous pensons que, chez ces Mouches stabilisées, s'établit un équilibre héréditairement stable entre le virus et les cellules de l'hôte. Le virus est alors transmis comme un constituant cellulaire normal sans que soit nécessaire une réinfection à chaque génération.

Cette hypothèse de "l'intégration" a été consolidée par la découverte de certaines souches de *Drosophiles*, appelées " $\rho$ ", qui possèdent à un point extrême les propriétés des souches stabilisées. Elles sont encore plus pauvres en virus infectieux, la multiplication du virus y est encore plus freinée et elles ne sont presque jamais sensibles au  $\text{CO}_2$ . Ces propriétés sont héritées maternellement de façon stable.

Il se pourrait que la latence observée chez de nombreux Insectes, tels que les Lépidoptères, soit l'équivalent de cette stabilisation ou intégration que nous supposons exister entre le virus  $\sigma$  et les cellules de la *Drosophile*.

Dans le cas du virus de la *Drosophile*, la latence ne peut être reliée à la perte du pouvoir infectieux de l'insecte qui n'existe pas. On peut cependant remarquer que les *Drosophiles*  $\rho$ , chez lesquelles la latence est la plus poussée, ne présentent plus les symptômes caractéristiques de la sensibilité au  $\text{CO}_2$ .

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# Evidence of Adaptive Races Among Oriental Fruit Moth Parasites

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## ABSTRACT

Within the past 50 years the oriental fruit moth has become established in several widely separated areas. In each of these, except possibly in Japan, numerous native parasite species have rather quickly become adapted to parasitizing it. The adaptation has not progressed so far that the parasites can multiply perennially and exclusively on the new host, which may be the reason that colonization of these species in countries far from their native habitats has been generally unsuccessful.

In North America there are more than 100 species of insect parasites which attack the oriental fruit moth. A score or more are sufficiently adapted to be able to attack it as readily as any other known host. There is evidence that *Macrocentrus ancylivorus* Rohwer has progressively increased its capacity to parasitize the oriental fruit moth heavily over a wide area. This seems to be an example of an adaptive race arising naturally. The absence of immunity of the oriental fruit moth to attack by native parasites contrasts strongly with the condition which exists among many of our common foreign pests, to which very few parasites have become adapted during many years of close coexistence over wide areas.

At Moorestown, N.J. a laboratory strain of *Horogenes molestae* (Uchida) has become progressively better adapted to propagating in the potato tuberworm, *Gnorimoschema operculella* (Zeller), not known to be a natural host. When used in caged-tree tests the race adapted to the tuberworm has attacked oriental fruit moth as readily as those reared for several successive generations on the oriental fruit moth.

I am sure that many workers in biological control, from their own experience, have been long convinced that races or strains of less than species rank exist. A better understanding of such biological aggregates is important to the study and utilization of insect parasites.

## GENETICS OF NATURAL RACES

A species may be considered as a population of interbreeding individuals inhabiting a geographic area. Usually it consists of many millions of individuals distributed discontinuously in respect to the details of the terrain over hundreds of thousands of square miles. An insect species may continue to exist for millions of years; yet when groups from the whole population are abruptly confronted with a changed environment, a race that is well adapted to the new environment may become segregated in a very short time. How does it happen that a biological entity can be stable in respect to geologic time scales and yet so capable of rapid adaptation? I believe that the knowledge geneticists have gained on the mechanics of sexual reproduction provides a plausible answer, and sheds light on some of the problems and the undeveloped possibilities of biological control.

Within the population of a species heredity is determined by the genes distributed in the chromosomes, which are so divided within each new generation of germ cells that species stability is insured. Presumably there are in all natural populations many kinds of genes. These insure variability, the probability of which is greatly increased by the mechanics of mitosis, meiosis, and fertilization, so that there exists great diversity in the recombinations of genetic material.

Within the last few years Dobzansky, Epling, and other workers, studying natural populations of certain species of *Drosophila*, have found that in some species chromosomal races coexist in natural populations in which the races have a nonrandom distribution. This aspect of their work has been summed up by Paterson and Stone (1952) as follows: "Thus it is very clear that genetic differences exist and can be demonstrated in populations of the same species which fit certain segments of the general population (sometimes local populations, sometimes chromosome races) to a certain ecological



environment, and so in turn affect the geographical distribution of species and even of chromosomal or other races within the species."

When an insect pest becomes established in a new area and multiplies to an abnormally large population, it causes an abrupt biological change in the environment for the many species of parasites that are native to that area. If the population of a parasite species includes no individuals that will attack the new pest, or if no normal progeny result from such an attack, successful parasitism will not ensue. However, there may be instances where some individuals of a parasite species attack the new pest successfully, either at the initial point of infestation or at some other locality as its distribution expands. If conditions are favorable for the propagation of the particular gene combination that permitted the first successful attack on the new host, parasitism will increase until some point of equilibrium is reached.

### IMPORTATION AND COLONIZATION FROM AREAS WHERE THERE MAY BE NATURAL RACES

The evidence that chromosomal races exist which have an irregular geographic distribution is an important factor in planning the importation, propagation, and colonizing of beneficial insect parasites. Since in many climatic and biological aspects the area to be colonized is an essentially new environment to the parasites being colonized, the presence of an abundance of the natural host may not be all that is needed. Let us assume that colonization will be successful only if there occurs in the parasite a favorable gene combination we shall term "A." In this discussion we have excluded the potential for mutation, which might be a factor in some species where this potential is relatively great and the populations are very large. We shall also assume three different locations: (1) one in which "A" is not present, (2) another in which "A" occurs in 1 out of 1000 individuals, and (3) a third in which "A" is found in 1 out of 100 individuals (Fig. 1). Importation and colonization of any number from the

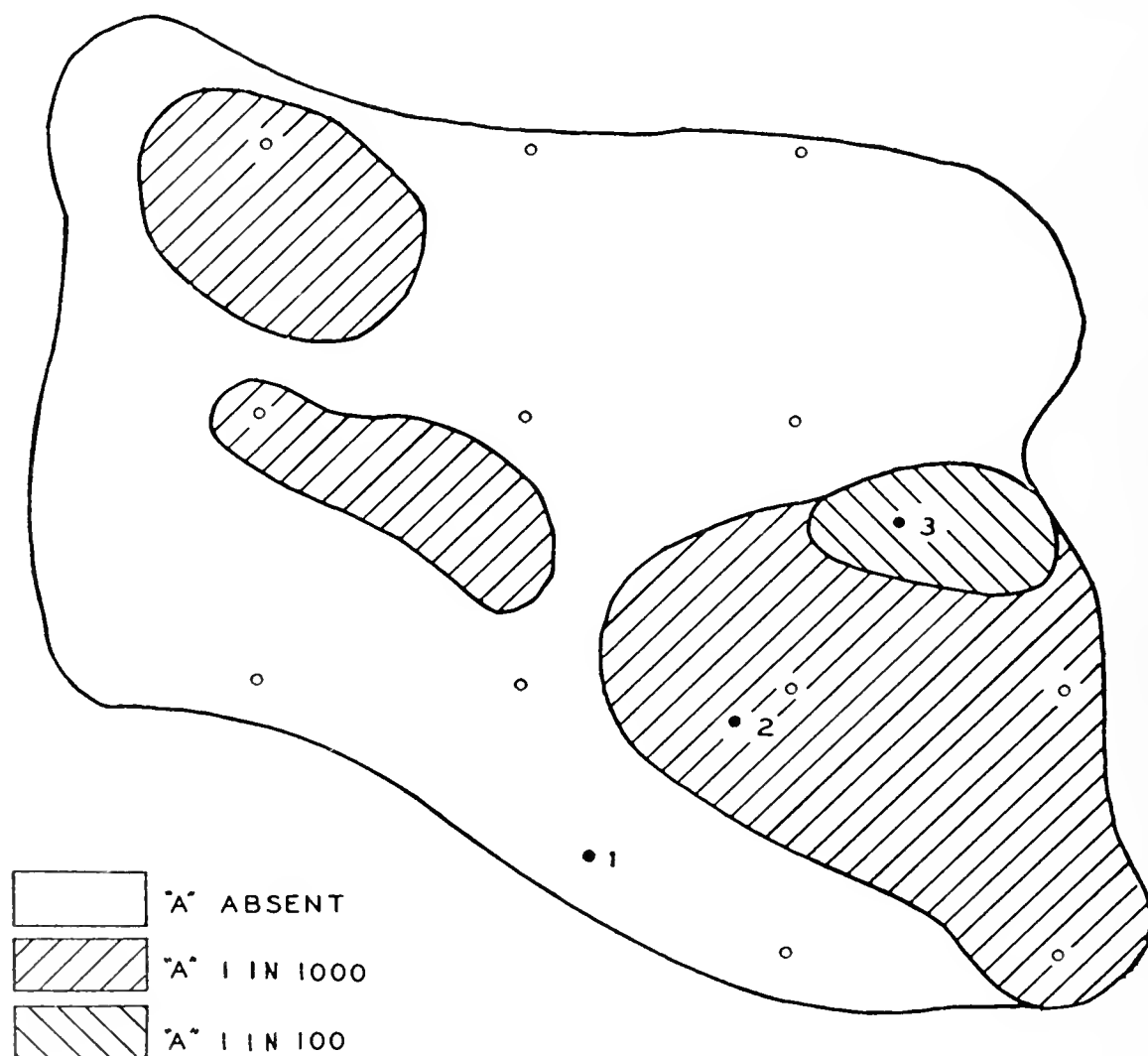


Fig. 1.— Schematic map of an area in which some hereditary quality necessary to successful importation of a parasite is irregularly distributed. The three dots (.) show hypothetical collection stations: 1 in area where "A" is absent, 2 in area where "A" occurs in 1 of 1,000 individuals, and 3 in area where "A" occurs in 1 of 100 individuals. The 12 circles represent a grid in which the spaces are too great to be likely to include stations in the area where "A" is present in 1 to each 100 individuals.

first location will be unsuccessful. Colonization of several thousand from the second location and of several hundred from the third location is likely to succeed. If propaga-

tion was started with considerably less than 100 individuals, even from the third location, it is possible that "A" would be lacking and colonization of individuals propagated from them would not succeed even though very large numbers were released. Explorers without any information as to the distribution of "A" would be likely to strike some localities where it is present by collecting material from several scattered stations, although they might miss the section where it occurs in the 1 to 100 ratio except through a closely spaced grid of many stations. A grid of 12 such stations might still miss this section as it does in Fig. 1. Any larger number of stations would be likely to include it.

The work with *Agathis festiva* Mues., one of the recently imported parasites of the oriental fruit moth (*Grapholitha molesta* (Busck)), illustrates well a procedure in which the chances for successful introduction have been unduly reduced. Since this parasite was obtained unexpectedly from a single small shipment from the only locality in which it is now known to occur, and which is inaccessible to us, the unfavorable conditions have been beyond our power to alter. The importation was limited to two mated females (Fig. 2). They have been successfully propagated and tens of thousands colon-

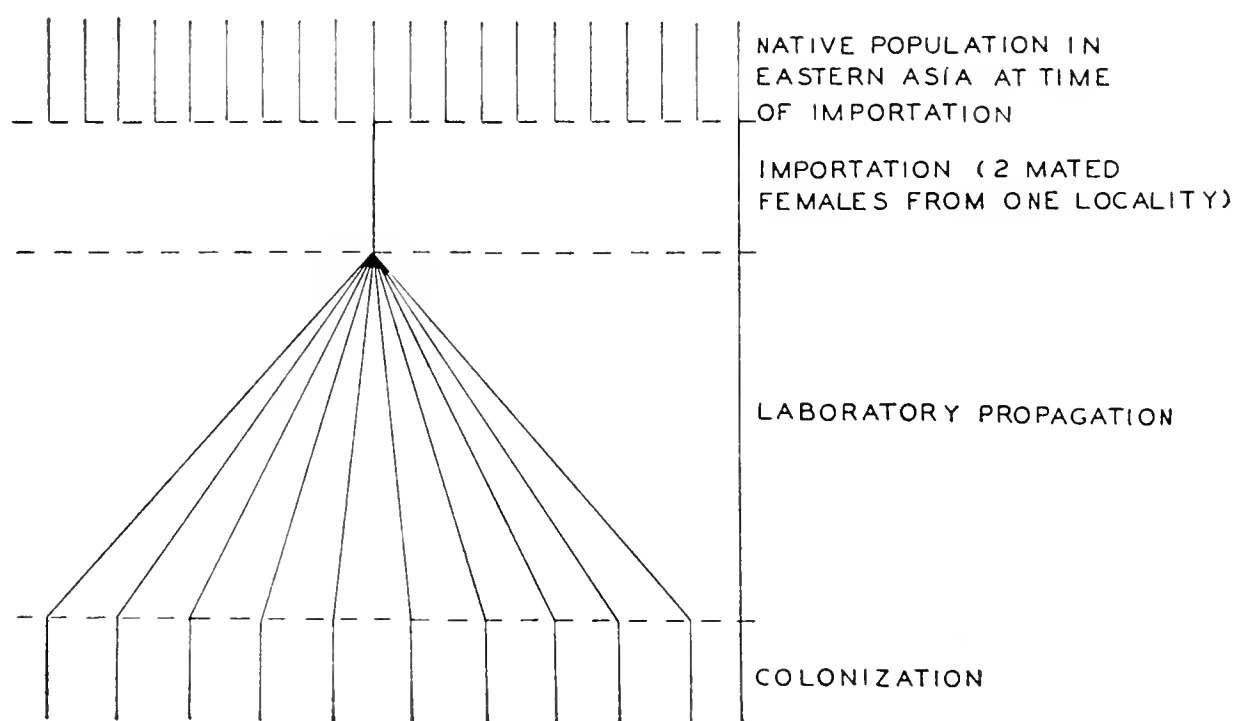


Fig. 2 — Schematic representation of the importation, propagation, and release of *Agathis festiva* Mues. in which the native population was poorly represented.

ized. Our stock approximates a closely inbred line, with little chance of obtaining a fair representation in it of the genetic variation existing within the species. The chances for successful colonization would be much increased by importation of large numbers from several environments. Also, if the parasites used in colonization are to be propagated in the laboratory, an effort should be made to obtain the broadest possible hybridization of the stock used for breeding.

### UNUSUAL NATURE OF ORIENTAL FRUIT MOTH PARASITISM

I should like to present now some data which seem to show that among the parasites of the oriental fruit moth there is an unusual tendency to develop races adapted to this host, and an unusual lack of capacity to adapt themselves to new geographical areas.

By 1925, about 12 years after the oriental fruit moth had gained entry into the United States, 42 species of native parasites had been reported as attacking it (Stearns 1928). At present, about 43 years after its establishment, over 100 species of native parasites attack it in this country. When undisturbed by the use of organic insecticides, these parasites usually destroy a large portion of the population. By 1933, 13 years after the oriental fruit moth was first found in Europe, Haeussler (1933) reported that more than 30 species of native parasites were attacking it in France and Italy. He also observed that the rates of parasitization were low, not exceeding 6 percent for the twig-infesting larvae and 23 percent for the cocoons. This species has since spread to other European countries, and in some localities it is being attacked heavily by indigenous species of parasites not reported by Haeussler. In 1951 Baggiolini (1952) found a species of *Lissonota* parasitizing as high as 82 percent of the oriental fruit

moth in peach orchards in southwestern Switzerland. In Australia in 1932, about 18 years after the introduction of the oriental fruit moth, R. W. Burrell, of the United States Department of Agriculture, found 10 species of indigenous parasites attacking it. While the number of species was not large, the rates of parasitization were high, ranging from 33 to 88 percent. The small amount of information available to me regarding oriental fruit moth infestations in South America is sufficient to indicate that indigenous parasites are attacking it there also. In 1935, 6 years after it was first reported from Argentina (López Cristóbel 1935), it was being parasitized by 3 species of native parasites, and several others have since been found.

Haeussler (1940) found at least 60 species of parasites of the oriental fruit moth in Japan and Korea (Chosen) in 1932 and 1933. This moth was first noticed in Japan in 1902 or earlier, probably an introduction from its original home on the eastern Asiatic mainland. There is some uncertainty as to which of these parasites are indigenous to Japan, since 24 species were found in both Japan and Korea. Although some of the parasites may have come, like their host, from the Asiatic mainland, it seems probable that many of the 37 species found only in Japan became adapted to the oriental fruit moth after its arrival there.

In general, then, we find that the oriental fruit moth has acquired rather quickly numerous new parasites from among indigenous species. These new parasites have attacked it in substantial numbers wherever it has been introduced, with the possible exception of Japan, where the situation is not clear. This is a notable contrast to the record of some of the other introduced pests in the United States and Canada.

In 1929, about 60 years after the introduction of the gypsy moth (*Porthetria dispar* (L.)) and 30 years after the brown-tail moth (*Nygmia phaeorrhea* (Donov.)) had become established in the United States, Burgess and Crossman (1929) observed that none of the native parasites had attacked either to any considerable degree. About 27 years after infestations of the oriental moth (*Cnidocampa flavescens* (Wlk.)) were found in Massachusetts, Collins (1933) observed that it had rarely been parasitized by indigenous species. The satin moth (*Stilpnotia salicis* (L.)) was found in Massachusetts in 1920 and in the State of Washington in 1922. More than 15 years later Jones, Webber, and Dowden (1938) reported that native insect enemies were unimportant in both areas. Thirty-two years after the European corn borer (*Pyrausta nubilalis* (Hbn.)) was found in the United States, Baker, Bradley, and Clark (1949) reported that, although 29 indigenous species had been reared as corn borer parasites, none had been numerous enough to affect borer abundance, and none showed any tendency to become increasingly effective as corn borer parasites. The Japanese beetle (*Popillia japonica* (Newn.)), although it is about 40 years since it became established in the United States, is still remarkably free from native parasites.

Since 1930, 13 species of parasites of the oriental fruit moth from eastern Asia, 5 from Europe, and 2 from Australia have been colonized in the United States. Only one species is known to be established, and it is unimportant. *Macrocentrus ancyliivorus* Roh., the dominant North American parasite, was imported many years ago into France, Japan, Australia, and Uruguay, but so far as known it has failed to become established in any of these countries. The record of parasite introductions against the other insect pests mentioned above is conspicuously different. Foreign parasite species colonized in North American infestations of the gypsy moth, the brown-tail moth, the oriental moth, the satin moth, and the European corn borer have become firmly established and are now dominant in the biological control of these pests.

From these data we conclude that the indigenous parasites tend to become adapted quickly to the oriental fruit moth, a new host, but when they are colonized in distant geographical areas they display practically no capacity for adapting themselves to a new environment.

#### EVIDENCE OF ADAPTIVE RACES AMONG DIFFERENT SPECIES OF PARASITES

Are all the many species of native parasites that have acquired the oriental fruit moth as a new host during the last half century to be considered adaptive races? A majority of the more than 100 North American species recorded as parasites attack

this insect infrequently and in small numbers. Certainly, this occasional parasitization does not seem to be stimulating any hereditary tendency to attack this new host. They are not now recognizable as adaptive races.

About the score or more of parasites that attack it in moderate to large numbers, there is unfortunately a dearth of information during the years when the parasitism was first observed. For later years there is more information. The Moorestown (N. J.) laboratory in cooperation with several State agricultural experiment stations made a survey of the parasitism of twig-infesting larvae of this moth from 1931 through 1939. This survey included peach orchards in 216 counties in 20 States extending from Massachusetts to Illinois and south to Georgia and Arkansas. Hundreds of samples were taken each year. These data have been summarized in several ways. Table I

TABLE I. Percentage of all Localities Sampled from which Oriental Fruit Moth Parasites were Reared, 1931-9.

Parasite	1931-3		1934-6		1937-9	
	Range	Average	Range	Average	Range	Average
<i>Macrocentrus ancyliivorus</i>	32-39	33.7	44-51	47.7	54-68	63.0
<i>Macrocentrus instabilis</i>	6-11	8.0	12-13	12.3	16-39	24.3
<i>Eubadizon pleurale</i>	3- 4	3.7	10-13	11.7	5-31	14.7
<i>Macrocentrus delicatus</i>	22-27	24.0	24-29	27.0	19-59	35.0
<i>Cremastus minor</i>	5-20	12.3	11-16	14.0	7-29	19.7
<i>Horogenes obliteratus</i>	5- 8	6.3	2- 4	3.0	1-18	11.0
<i>Glypta rufiscutellaris</i>	35-40	37.0	26-40	34.7	28-50	39.3
<i>Pristomerus euryptychiae</i>	10-26	18.0	10-16	12.7	10-30	17.7

shows the percent of all localities sampled from which eight of the most common parasites were reared. Since there was considerable fluctuation from year to year, the data have been grouped in 3-year periods.

*Glypta rufiscutellaris* Cress. and *Pristomerus euryptychiae* Ashm. seem to have risen abruptly to high rates of parasitization over a wide area. Both were first reported as parasites of the oriental fruit moth in 1925 and were as abundant by 1931 as they have been since. There is some evidence of increasing parasitization by *Horogenes obliteratus* (Cress.), *Cremastus minor* Cush., *Macrocentrus delicatus* Cress., *Eubadizon pleurale* Cress., and *Macrocentrus instabilis* Mues., this increase becoming progressively more apparent from the first to the last named. *Macrocentrus ancyliivorus* Roh. became the most commonly reared parasite in 1933, and steadily increased in its rate of occurrence during the nine-year period. One interpretation of these data is that in the whole population of this species there was a steady increase of a race adapted to parasitizing the oriental fruit moth. It is possible that similar adapted races are emerging from some of the other species, but at a slower rate. Boyce and Dustan (1954) have shown that in Ontario, north of the area covered by our observations, the rate of parasitization by *M. delicatus* increased from 1939 to 1953. In *G. rufiscutellaris* and *P. euryptychiae*, which seem to have jumped quickly to high rates of parasitization at many places in the newly infested area and not to have progressed subsequently, it is not likely that there are adapted races.

Let us review briefly the history of *Macrocentrus ancyliivorus*, which has become more conspicuously adapted to the oriental fruit moth than any of the other North American parasites. The species was widely distributed in the United States and had been reared from various lepidopterous hosts (Muesebeck 1932) before the introduction of the oriental fruit moth. It has not been found native to any other part of the world, and it is almost certainly indigenous to North America. In 1920 it was found to be heavily parasitizing the strawberry leaf roller (*Ancyliis comptana fragariae* (W & R.)) in New Jersey (Fink 1926). By 1925 it was heavily parasitizing the oriental fruit moth in New Jersey (Stearns 1928), and also attacked this insect in several of the earlier infested sections from northern Virginia to southern Connecticut. In the early 1930's it did not occur as a parasite of the oriental fruit moth over a large portion of the newly infested area.



Through work started in 1930 *M. ancyliivorus*, obtained principally from strawberry leaf rollers collected in New Jersey, was intensively colonized from Massachusetts to Michigan and south to Arkansas and Georgia. The species was recovered immediately as a parasite of the oriental fruit moth in many localities where it had been colonized. Within three years it became the dominant parasite of this pest in the Eastern States, and continued to expand its distribution and to increase its rate of parasitization. Apparently, at some time between 1916 and 1925, a race well adapted to attacking the oriental fruit moth emerged from the general population of this parasite somewhere between Washington, D. C., and New Haven, Conn. Assisted by widespread liberations, it rapidly became the dominant parasite over most of the area infested by this insect in the United States.

*Horogenes molestae* (Uch.), a common parasite of the oriental fruit moth in Japan, has provided us with additional information on adaptive races. In 1949 a few adults were reared from oriental fruit moth cocoons imported from Japan. An attempt was made to propagate this parasite on the potato tuberworm (*Gnorimoschema operculella* (Zell.)), an unnatural host. In the first five lots exposed there was a total emergence of 3,130 hosts and parasites, of which only 14 were *Horogenes*. In this trial there was a return of only 0.07 parasite per female-day on 196 female-days' exposure, and a parasitization rate of only 0.4 percent. The parasites reared appeared normal, and the only obstacle to propagation was the females' lack of interest in the tuberworm. It was soon found that they could be induced to accept tuberworm by offering them halves of potato pinned to apple and stocked at the contact surface with a mixture of oriental fruit moth larvae and tuberworms. Subsequently the same effect was produced by spraying or rolling potato infested with young tuberworms with extracts of oriental fruit moth larvae. After about 11 successive generations had been propagated in this manner, evidence was obtained that a laboratory race was being developed which would attack the tuberworm freely without artificial stimulation. By the end of 1952, and after about 40 generations, the propagating rate per breeding female was 24 times as great as that obtained in the first attempt to propagate in the tuberworm in 1949. Further progress has been made in adaptation to laboratory breeding in the tuberworm. In 1953, after about 50 generations, 55,000 of these parasites were propagated on the tuberworm, and the production rate had increased to 13.2 females per breeding female or 197 (82 females) per pound of potato.

In tests on caged peach trees the progeny of the laboratory tuberworm strain of *Horogenes* parasitized the oriental fruit moth as effectively as did those from another stock propagated for several successive generations on the oriental fruit moth.

Although the rate of parasitization by *H. molestae* steadily increases when it is reared in the laboratory on the tuberworm, the reverse occurs with the oriental fruit moth. When reared continuously on the latter host, there is initially an excellent rate of increase, but this gradually falls off, and after about eight generations the laboratory strain becomes extinguished. This is similar to our experience in making liberations in many widely scattered locations in the Eastern States. In orchards there was at first an excellent rate of increase, but in following generations the number recovered became less until after a year or two the parasite could no longer be recovered. There may have been a need for alternating with some other host not available in the area colonized.

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# Éléments de la Spécificité parasitaire chez les Tachinaires

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## RÉSUMÉ

Parmi les Diptères du groupe des Tachinaires, certaines espèces n'attaquent qu'un seul hôte tandis que d'autres peuvent subsister aux dépens d'un grand nombre d'espèces phytophages appartenant parfois à des genres très divers.

De plus, les modalités de la reproduction chez les larvaevoridae présentent une grande variété de formes. Nous avons essayé de mettre en évidence les facteurs dont l'action pouvait expliquer l'existence d'une spécificité parasitaire plus ou moins stricte.

Nous avons pris des exemples chez les différents types éthologiques:

1) Tachinaires pondant des oeufs micro-types *Cyzenis albicans* (Fall.) et *Cténophorocera pavidus* (Meig.).

2) Tachinaires pondant des oeufs membraneux *Phryxe caudata* (Rond.) et *Carcelia processionae* (Ratz.).

3) Tachinaires à oeufs macro-types *Phorocera agilis* (R.D.)

4) Tachinaires à larves du type planidium *Ernestia rudis* (Fall.).

Nous avons examiné les possibilités de réalisation des phases successives du développement que nous avons classées de la manière suivante:

1) Rencontre du parasite avec un stade "sensible" de l'hôte.

2) Stimulation de la femelle conduisant au dépôt de l'oeuf.

3) Prise de possession de l'hôte par la larve parasite.

4) Evolution de la larve endo-parasite jusqu'à sa maturité.

5) Corrélation de cycles biologiques permettant la réalisation de générations successives.

Les obstacles rencontrés au cours des différentes phases du développement, soit du fait de l'activité de l'hôte, soit pour des raisons écologiques ou physiologiques, ont été examinés.

Cette étude nous conduit à insister sur l'importance des corrélations physiologiques hôtes-parasites.

## INTRODUCTION

La famille des Tachinidae constitue un des plus importants groupes d'Insectes Entomophages; elle comporte un nombre considérable d'espèces qui jouent un rôle de premier plan dans la limitation naturelle des populations de nombreux phytophages et dont plusieurs ont été utilisées dans différents essais de lutte biologique.

A l'intérieur de ce vaste groupe on note une très grande variété de types éthologiques notamment en ce qui concerne le mode de reproduction. La variation observée porte sur le type d'oeuf pondu, son mode d'incubation et également sur les modalités de la ponte.

En ne considérant que ce dernier caractère, on peut classer les différentes espèces en 3 groupes principaux, d'après la localisation de l'oeuf par rapport à l'hôte:

1) Espèces chez lesquelles la femelle introduit sa larve dans l'hôte: —  
ex. *Compsilura concinnata* (Meig.) (groupe VII de Pantel).

2) Espèces déposant leur oeuf sur l'hôte: —

On y distingue 2 types différents:

a) espèces pondant des œufs macrotypes sur le tégument de l'hôte (gros œuf à chorion épais déposé à un stade plus ou moins avancé de l'embryogénèse, groupe I de Pantel).

ex. *Phorocera agilis* (R.D.).

b) espèces pondant des œufs membraneux à chorion mince donnant immédiatement naissance à la larve du premier stade. (groupe VI de Pantel).

ex. *Phryxe caudata* (Rond.).

*Carcelia processioneae* (Ratz.).

3) Espèces pondant sur le feuillage: —

Là encore nous trouvons 2 types, très distincts, le premier rappelant dans une certaine mesure les formes à œufs membraneux, tandis que le second présente une originalité très spéciale. Ce sont:

a) les espèces pondant des œufs à éclosion immédiate d'où sortent des larves du type planidium (groupe IV de Pantel) qui s'attachent à l'hôte lors de son passage.

ex. *Ernestia rudis* (Fall.).

b) les espèces pondant des œufs microtypes destinés à être ingérés par les chenilles hôtes (groupe II de Pantel).

ex. *Ctenophorocera pavidata* (Meig.).

*Cyzenis albicans* (Fall.).

Notons encore qu'à l'intérieur de ces différents groupes on peut observer d'importantes différences éthologiques.

C'est ainsi que, chez les formes à œufs membraneux que nous avons eu l'occasion d'étudier, *Phryxe caudata* (Rond.) dépose son œuf au contact direct du tégument de l'hôte par allongement de l'ovipositeur et après avoir sélectionné un emplacement (Biliotti 1956) tandis que chez *Carcelia processioneae* (Ratz) il n'y a pas allongement de l'ovipositeur et l'œuf est projeté en direction des poils tégumentaires de l'hôte (observations non publiées).

Le nombre d'hôtes utilisés par les différentes espèces varie dans une très large mesure et sans relation directe avec le groupe éthologique auquel elles appartiennent. Il y a tous les intermédiaires entre le cas de *Compsilura concinnata* pour laquelle le catalogue de Thompson cite 203 espèces hôtes appartenant à 133 genres de 24 familles de Lépidoptères et d'une famille d'Hyménoptères (Tenthredinidae) et celui de *Phryxe caudata* que nous considérons avec L. P. Mesnil comme parasite spécifique de *Thaumetopoea pityocampa* (Schiff.). Il reste d'ailleurs beaucoup à faire pour établir la liste des hôtes de très nombreuses espèces.

L'intérêt des phénomènes de Spécificité parasitaire, aussi bien du point de vue des études biologiques que de celui de l'utilisation pratique des entomophages a été fréquemment souligné par de nombreux auteurs et W. R. Thompson (1951) dans une publication récente a pu écrire: "the understanding of what we call specificity is one of the most important problems involved in the scientific investigation of biological control and in attempts to establish this phase of economic entomology on a scientific basis".

Un certain nombre d'investigations expérimentales ont été consacrées à l'étude des différents aspects du problème de la Spécificité parasitaire mais la plupart d'entre elles ont porté sur les Hyménoptères. Le but de cette note est d'essayer de sélectionner les facteurs écologiques, éthologiques ou physiologiques, dont l'action peut expliquer qu'un phytophage soit un hôte occasionnel ou constant d'une Tachinaire donnée.

C'est par l'étude approfondie de chacun d'entre eux que nous pourrions espérer expliquer comment a pu se développer une spécificité parasitaire ou dans quelle mesure de nouvelles combinaisons hôte-parasite pourront être envisagées pour le contrôle biologique d'un ravageur.

Notre exposé ne présentera pas séparément les différents types de facteurs en cause, il est conçu suivant l'ordre chronologique de leur intervention. Les exemples choisis sont pris parmi les Tachinaires que nous avons eu l'occasion de rencontrer au cours d'études biocénétiques sur diverses chenilles défoliatrices et nous exposerons quelques résultats préliminaires obtenus expérimentalement sur les changements d'hôte de ces espèces.

## ANALYSE DES FACTEURS

Nous examinerons successivement les étapes qui doivent être franchies pour qu'une chenille devienne l'hôte normal d'un Tachinaire, nous les avons classées en 5 phases:

1) RENCONTRE DU PARASITE AVEC UN STADE "SENSIBLE" DE L'HÔTE: Nous ne développerons pas de considérations relatives à cette condition indispensable du développement, elles correspondent à ce que Thalenhorst (1950) a analysé sous le nom de "coïncidence". Les facteurs en cause sont essentiellement écologiques mais des processus physiologiques sur lesquels nous reviendrons au paragraphe 5 peuvent aussi intervenir.

2) STIMULATION DE LA FEMELLE CONDUISANT AU DÉPÔT DE L'ŒUF: Ici interviennent plus spécialement les facteurs éthologiques et physiologiques qui règlent le "comportement de ponte" de la Tachinaire adulte. Chacun des groupes que nous avons cités au début mérite de ce fait une étude spéciale et il est même probable qu'à l'intérieur de chacun d'eux d'intéressantes variations peuvent être mises en évidence.

Un récent travail de Monteith (1955) apporte une intéressante contribution à l'étude de ces phénomènes chez *Drino bohemica* (Mesn.) en s'attachant surtout à l'influence des stimuli olfactifs, gustatifs et chimiques; il étudie également l'influence du "conditionnement" préalable à un hôte donné ou à la plante nourricière de cet hôte, principalement du point de vue olfactif. La conclusion de son étude est que les phénomènes de conditionnement paraissent avoir peu d'influence sur la formation des races de *D. bohemica*.

Au cours de nos premières expériences réalisées sur des espèces à œufs microtypes (*C. pavidus*, *C. albicans*) à œufs membraneux (*C. processioneae*, *P. caudata*) ou à larve planidium (*E. rudis*) nous avons constaté l'influence prépondérante de l'état physiologique de la pondeuse. Chez ces espèces le développement embryonnaire a lieu à l'intérieur de l'utérus de la femelle, considérablement distendu et plein d'œufs. Lorsque les Tachinaires sont gardées longtemps en élevage dans de bonnes conditions mais sans qu'on les mette en présence de leur hôte, elles ont tendance à expulser les œufs murs, sur des supports quelconques. Chez les espèces à œufs microtypes on peut ainsi récolter facilement sur les parois du récipient d'élevage une quantité d'œufs murs correspondant à la quasi totalité de ceux que la femelle était capable de produire. Chez *P. caudata*, les œufs membraneux peuvent être pondus sur un support quelconque ou, de préférence, sur d'autres individus de l'espèce dans les élevages groupés (Biliotti 1956).

Aussi, lorsqu'on étudie le comportement de ponte doit-on opérer avec des Mouches présentant un degré uniforme de développement et commencer l'expérimentation avant que l'utérus soit entièrement plein d'œufs prêts à être expulsés. Les conditions écologiques indispensables à l'activité des Mouches aussi bien que l'attraction exercée sur elles par diverses chenilles, ou différents types de feuillages, varient à mesure que le contingent d'œufs murs s'accroît.

Chez *P. caudata* les femelles privées de leur hôtes normal déposent facilement leurs œufs prêts à éclore sur une grande variété de chenilles. Au laboratoire nous avons obtenu la ponte sur: *Thaumetopoea processionea* (L.), *Euproctis chrysorrhoea* (L.) (= *phaeorrhoea* Don), *Diloba coeruleocephala* (L.), *Operophtera brumata* (L.), *Colotois pennaria* (L.), *Malacosoma castrensis* (L.), *Malacosoma neustria* (L.), *Triphaena pronuba* (L.), *Pieris brassicae* (L.) dont les chenilles présentent des types morphologiques très différents et qui appartiennent à des familles éloignées les unes des autres du point de vue systématique.

Chez *C. processioneae* il est plus difficile d'obtenir la ponte sur l'hôte inhabituel sauf si la femelle a d'abord été mise en présence de chenilles de *Thaumetopoea processionea* (L.) et si l'hôte proposé est lui-même fortement pileux. Dans certains cas, nous avons pu obtenir des pontes sur un pinceau promené devant la Mouche.

3) PRISE DE POSSESSION DE L'HÔTE PAR LA LARVE PARASITE: L'entrée de la larve de Tachinaire dans le corps de son hôte est évidemment fonction du type d'œuf pondu et du lieu de ponte. Chez *C. concinnata* la larve du premier stade est placée par la femelle au lieu même où elle doit commencer son développement. Chez les espèces à



œufs microtypes il est indispensable que l'œuf éclore normalement dans le tube digestif de l'hôte. D'autres auteurs (Severin *et al.* 1915) ont indiqué les facteurs qui permettent d'obtenir cette éclosion; dans nos expériences réalisées avec *C. pavidus* et *C. albicans* il nous a paru indispensable que le chorion de l'œuf soit éclaté lors du passage entre les mandibules. La larve du premier stade paraît apte à se libérer elle-même de la membrane vitelline. La forme et la taille des pièces buccales de l'hôte interviennent donc dans le processus (caractère spécifique et variation au cours des stades larvaires successifs). Les déplacements ultérieurs de la larve microtype seront envisagés au paragraphe suivant.

Chez les espèces à œufs Macrotypes la jeune larve pénètre en général au lieu même où l'œuf a été déposé, mais comme l'évolution embryonnaire n'est pas achevée au moment de la ponte, il arrive que l'hôte subisse une mue avant que la pénétration ait pu avoir lieu.

Chez les formes à œufs membraneux la larve doit fréquemment se déplacer avant de trouver un point de pénétration tandis que les larves du type Planidium sont obligées d'attendre le passage de l'hôte pour s'accrocher à lui avant de l'envahir. Pendant cette phase plus ou moins longue de vie à l'extérieur, la larve est soumise aux variations des facteurs climatiques qui peuvent l'affecter plus ou moins ainsi qu'aux réactions possibles de l'hôte.

Nous en avons observé fréquemment dans le cas de *P. caudata* et *C. processioneae*. Au moment où la larve parasite attaque les téguments de l'hôte à l'aide de son armature buccale, la chenille peut la détruire avec ses mandibules ou encore la faire tomber de son corps en s'agitant violemment. Ces réactions ne sont pas toujours le fait d'hôtes inhabituels, ainsi chez *T. processioneae* par exemple, on en observe assez fréquemment, surtout chez les chenilles des derniers stades larvaires, lors de la pénétration du parasite subspécifique *C. processioneae*. Par contre la pénétration de *P. caudata* dans *T. pityocampa* ne provoque généralement aucune réaction. Ces gestes de défense ne sont d'ailleurs pas constants pour une espèce, ni pour un individu donné, c'est ainsi que nous avons pu observer des chenilles d'*E. chrysorrhoea* détruisant successivement plusieurs larves de *P. caudata* pour se laisser ensuite envahir passivement par la suivante. Il en est de même des réactions de l'hôte contre les femelles pondeuses lorsque celles-ci viennent à son voisinage. Les mouvements parfois violents du corps des chenilles ne sont pas suffisants pour décourager complètement la Tachinaire, ils peuvent réduire la fréquence des cas de parasitisme pour deux espèces données mais ne peuvent être considérés comme une cause régulière de protection d'un phytophage, au moins pour celles que nous avons examinées.

Il nous paraît par contre beaucoup plus intéressant d'étudier le comportement des jeunes larves pénétrant activement dans l'hôte au cours des phases successives que comporte cette opération (exploration, percement des téguments, pénétration proprement dite). L'activité de percement de la cuticule de l'hôte a été obtenue avec *C. processioneae* en utilisant des hôtes aussi différents que *Bombyx mori* (C.), *Pieris brassicae* (L.) *Alsophila aescularia*; elle ne paraît pas liée aux caractères du tégument mais à une source de stimulation plus interne puisque nous ne l'avons jamais obtenue sur des exuvies.<sup>1</sup>

4) ÉVOLUTION DE LA LARVE ENDOPARASITE JUSQU'À SA MATURITÉ: Les modalités de la vie larvaire diffèrent profondément d'une Tachinaire à une autre. Si la plupart des espèces à œufs macrotypes passent leur vie larvaire à l'intérieur de la gaine développée au point de pénétration (jusqu'à la phase sarcophage du 3ème stade larvaire), on rencontre dans les autres groupes des successions plus ou moins complexes de phases de vie libre, de vie à l'intérieur d'un organe ou d'un tissu déterminé, et de vie à l'intérieur d'une gaine développée sur un "soupon cutané ou trachéen secondaire".

Les réactions de l'hôte peuvent se manifester dès la pénétration de la larve parasite. Elles sont alors de 2 ordres:

CICATRISATION rapide empêchant les échanges respiratoires de la larve. C'est le cas observé par Mesnil et d'Aguilar (1945) lorsque *Macquartia grisea* (Fall.) attaque

<sup>1</sup> Il est évident que la morphologie du tégument joue un rôle considérable dans la limitation des possibilités mécaniques de pénétration et doit être étudiée aussi bien dans son aspect spécifique que dans sa variation en fonction des stades larvaires.

le Doryphore; c'est également ce qu'a observé Tadic (1955) dans le cas de *Mericia ampelus* (Wlk.) parasitant *B. mori* (dans ce cas il y a encapsulage ultérieur du parasite).

ENKYSTEMENT de la larve parasite par suite de l'activité phagocytaire de l'hôte.

De telles réactions que certains auteurs ne croyaient possibles que vis-à-vis de larves malades ou mortes, peuvent en réalité se produire de façon très précoce et entraîner la mort du parasite. Strickland (1923, 1930) étudiant le cas de *Gonia capitata* (Fall.) parasitant *Porosagrotis orthogonia* (Mon.) a constaté sur la jeune larve qu'elle était très fréquemment enkystée dès qu'elle quittait la paroi du mesenteron pour gagner la cavité générale (*G. capitata* est une espèce à œuf microtype dont la larve éclot dans l'intestin et passe un temps variable dans la paroi du mésenteron). Par contre si la larve réussit à gagner les ganglions nerveux céphaliques elle y demeure un certain temps et repasse ensuite dans la cavité générale sans éveiller aucune réaction phagocytaire. Nos propres observations portant sur des espèces à œufs membraneux nous ont montré la possibilité d'enkystements précoces pour *C. processioneae* et *P. caudata*. La morphologie des kystes obtenus répondait à ce qui a été observé par Schneider (1950a) et par Salt (1956) dans le cas de parasites hyménoptères.

N'ayant pas fait d'étude histologique, nous nous contentons d'en distinguer 2 types suivant qu'il y a ou non apparition d'une couche mélanisée. Le Tableau I résume nos observations.

TABLEAU I. Enkystement de la Larve primaire libre chez différents Hôtes.

Parasite	Kyste sans mélanisation	Kystes avec mélanisation
<i>C. processioneae</i>	<i>Malacosoma castrensis</i>	<i>Mamestra brassicae</i> <i>Vanessa Io</i> <i>Pieris brassicae</i> <i>Eriogaster lanestris</i>
<i>P. caudata</i>	<i>M. castrensis</i>	<i>Colotois pennaria</i> <i>P. brassicae</i> .

Pour *C. processioneae* l'enkystement peut aussi atteindre une larve ayant déjà pénétré dans un lobe adipeux. C'est le cas parfois chez *M. brassicae* (kyste non mélanisé) et chez *B. mori* (mélanisation).

Nos expériences ont été réalisées soit en obtenant directement la ponte sur l'hôte inhabituel soit en transportant des jeunes larves déposées sur un hôte normal.

La formation d'un type déterminé de kyste est une propriété de l'hôte et on peut observer des remaniements du matériel phagocytaire après la mort du parasite.

Chez *P. brassicae* les kystes mélanisés sont rejetés lors d'une mue.

En dehors des réactions phagocytaires, les larves à leur pénétration peuvent être détruites si l'hôte est en période d'exuviation, nous avons observé ainsi des larves de *P. caudata* mortes dans le liquide exuvial chez *T. pityocampa*.

Le fait qu'une larve primaire n'ait pas provoqué de réactions phagocytaires n'est en aucune manière le signe que la totalité du développement larvaire pourra s'effectuer dans l'hôte.

Les larves de *P. caudata* peuvent rester vivantes pendant longtemps dans la cavité générale d'*E. phaeorrhoea* mais finissent par y périr avant d'avoir formé leur "soupon trachéen secondaire", dans ce cas c'est le cadavre qui peut être enkysté.

Lorsque *P. brassicae* ingère les œufs de *C. pavidata* l'éclosion de ces derniers est normale et les larves gagnent les glandes séricigènes où devrait s'effectuer la 2ème phase de leur développement, mais, arrivées là, elles sont incapables de réaliser leur croissance normale et meurent plus ou moins précocement en provoquant une dégénérescence locale de la glande. Des fragments de glande contenant la larve morte du parasite peuvent être retrouvés dans le papillon qui éclot normalement.

Lorsqu'on fait parasiter *T. processionea* par *P. caudata* la larve primaire, après une phase de vie libre dans la cavité générale de l'hôte va percer son "sopirail secondaire" sur les buissons trachéens des 2 derniers stigmates abdominaux ce qui correspond au comportement normal chez *T. pityocampa*. Mais, à partir de ce moment, la croissance de l'hôte est perturbée et la chenille finit par mourir après une longue période d'inanition. La larve primaire du parasite survit quelques jours dans le cadavre puis finit par mourir à son tour.

Pour *M. neustria* le développement se poursuit encore plus loin comme nous l'avons déjà signalé. (Biliotti 1956).

En définitive le succès du parasitisme ne peut être assuré que par la réalisation des étroites corrélations physiologiques hôtes-parasites qui marquent le développement normal.

5) CORRÉLATION DES CYCLES BIOLOGIQUES PERMETTANT LA RÉALISATION DES GÉNÉRATIONS SUCCESSIVES: En fait, les considérations relatives à cet aspect des relations parasitaires auraient pu être exposées au paragraphe 1, mais nous voulons essentiellement parler ici de l'existence de mécanismes physiologiques régulateurs permettant à un parasite de retrouver toujours son hôte à chaque génération. Ces faits découlent des corrélations physiologiques évoquées au paragraphe précédent.

Nous avons déjà noté (Biliotti 1955), chez *P. caudata* qu'une diapause de l'hôte induisait celle du parasite. Des phénomènes du même ordre avaient été vus par Pantel dans le cas de *P. brassicae* parasité par *C. concinnata* mais il les interprétait comme un effet des conditions climatiques. D'autres auteurs ont également mis en évidence des corrélations de même ordre notamment Mellini dans le parasitisme de *Phytomyptera nitidiventris* (Rond.) sur *Pterophorus microdactylus* (Hbn.).<sup>2</sup>

Mais il est des cas où la corrélation est obtenue de façon moins directe. Chez *C. processioneae*, la larve du 3ème stade subit une diapause dont la durée équivaut à l'ensemble de la vie nymphale, de la vie imaginale et du développement embryonnaire de l'hôte. Ce dernier subit de son côté une diapause au stade d'embryon prélarvaire. Le jeu de ces 2 mécanismes apparemment indépendants assure pour chaque génération l'apparition des Mouches après l'éclosion des jeunes chenilles.

## CONCLUSION

De cette analyse rapide nous retiendrons qu'une grande variété de facteurs aussi bien morphologiques qu'écologiques, éthologiques ou physiologiques doivent être étudiés pour expliquer le succès du parasitisme d'une Tachinaire sur un hôte donné.

L'importance primordiale des corrélations physiologiques hôte-parasite peut seule expliquer la réalisation des cas de spécificité étroite. Dans le cas des espèces à exigences moins strictes le jeu des autres facteurs en cause rend facilement compte du fait qu'une espèce soit erratique ou "élective" au sens de Faure (1926).

De toute façon il nous manque encore beaucoup d'informations sur les possibilités de développement des différentes espèces dans les conditions naturelles et les principaux points mis en évidence dans notre revue demandent une étude expérimentale détaillée.

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<sup>2</sup>Chez les Hyménoptères ces phénomènes ont été remarquablement étudiés par Schneider (1950b).

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# Selective Breeding to Improve Adaptations of Parasitic Insects<sup>1</sup>

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## ABSTRACT

*Parasitic insects usually exhibit a narrow range of adaptation to environmental conditions. This limits the possibilities of success in introduction programs. Lack of adaptation among parasites includes among other things poor climatic tolerance, lack of synchronization between host and parasite biologies, failure to recognize the host environment, and inability to survive on the host on certain host plants. Races or strains of parasites differing from one another in important respects are fairly commonplace in nature. This offers encouragement for similar developments in the laboratory through selective breeding. The successful development and use of an improved strain involves (1) determination of characters needing improvement, (2) presence of or provision for adequate genetic variability, (3) adequate selection procedures, and (4) maintenance of integrity of the new strain in the field. Some results of selective breeding with insect parasites are discussed.*

## INTRODUCTION

The majority of parasites introduced in biological control programs fail to become established. Of those which do, only a relatively few successfully regulate host populations at low densities. According to Clausen (1936), about 18% of the entomophagous species imported into the United States between 1883 and 1936 and about 34% of those imported into Hawaii, became established. Only a relative few of those established were highly successful.

Parasitic species which fail to become established or which become established but do not control the host successfully, nevertheless may be intrinsically highly efficient parasites. A distinction should be made between parasites which are intrinsically capable of maintaining the host at low population levels (that is, which have high searching capacities) but fail because of poor adaptation to certain conditions in the new environment and parasites whose searching ability is such that they can exist only at high host population levels. These different abilities can most easily be determined in the native home of the species in question. In any event, the species with a high searching capacity but poor environmental adaptation offers the greatest promise for improvement through selection, inasmuch as it already possesses the most important general quality necessary in a successful parasite.

## OCCURRENCE OF ADAPTIVE WEAKNESSES IN NATURE

The fact that most species of imported parasites do not become established is a priori evidence of their rather close adaptation to a limited range of environmental conditions. A serious lack of adaptation is obvious, it does not have to be proved. However, the actual reason why a parasite fails to become established or to control the host is often quite obscure, especially in cases where the new environment closely resembles that of the native home.

Very minor changes in the regular environment of a parasite species can be critical. Slight climatic differences may be responsible for failure, or the cause could lie in obscure biological relationships such as differences in host plant physiology affecting host-insect physiology, with the resulting biochemical composition of the host rendering it unsuitable nutritionally for development of the parasite.

In a given environment a host-parasite interaction may result in, say, an average degree of natural control. Shift the environment in one direction and the host may be favored over the parasite to the extent of becoming a pest; shift it in the other direction and an excellent degree of natural control may be attained. Various examples of this are recorded in the literature.

<sup>1</sup> Paper No. 1008, University of California Citrus Experiment Station, Riverside, California

Many years ago several workers (Glenn, 1909; Hunter, 1909; Webster & Phillips, 1912; Headlee, 1914) obtained data to indicate that population increase of the grain aphid or greenbug, *Toxoptera graminum* (Rond.), was favored over its principal parasite, *Lysiphlebus testaceipes* (Cress.) (*tritici* Ashm.), by certain weather conditions. Low temperatures, in particular, were more unfavorable to the parasite than to the aphid. The aphid was able to oviposit at lower temperatures than the parasite and it developed more rapidly and showed better survival at lower temperatures than the parasite. Warm weather was more favorable to the parasite than to the aphid. Dunn (1952) obtained similar results with a predator. At temperatures below 50°F. aphid populations increased markedly and the coccinellid predator lagged behind, whereas during the summer the coccinellid was able to overtake and reduce the aphid populations.

Payne (1933), after a detailed laboratory study on the effect of temperature and humidity on the Mediterranean flour moth, *Ephestia kühniella* Zell., and its parasite, *Microbracon hebetor* Say, concluded that, in general, high temperatures (above 32°C.) favor the parasite and low temperatures (15°C. and below) favor the host. At 15°C. the parasite was sometimes able to overtake the host, sometimes not. Below 15°C. there was no possibility of the parasite catching up with the host. At temperatures above 32°C. the parasite had a decided advantage over the host.

Burnett (1949) has nicely illustrated similar trends experimentally. Working with laboratory populations of *Trialeurodes vaporariorum* (Westwood) and its parasite *Encarsia formosa* Gahan, he showed that different mean temperatures result in quite different population interactions between the host and parasite. At 18°C. the host increased more rapidly than the parasite population; at 24°C. host and parasite rates of increase were about equal, whereas at 27°C. the parasite population increased more rapidly than that of the host until it dominated the host. Other instances illustrative of various situations in which a parasite might fail to become established, or successfully control the host, follow:

Flanders (1940) is of the opinion that lack of adaptation owing to direct climatic influence is not as important as that owing to other ecological factors. He states: "A parasitic species may fail to become established because it does not frequent host habitats or because it frequents habitats which lack hosts . . . Establishment may fail if the deposition of fertilized eggs by colonized adult parasites is inhibited by a change in condition of the host . . . or the lack of food; or if the development of the parasite progeny is inhibited by the unsuitability of its normal host . . ."

Lack of necessary alternate hosts may limit the success of parasites. Clausen, King & Teranishi (1927) felt that the successful establishment of *Campsomeris annulata* (F.) on *Popillia japonica* Newm. would depend upon the abundance of alternate hosts. Howard & Fiske (1911) thought that the failure of *Apanteles fulvipes* (Hal.) to become established on the gypsy moth was owing to the lack of an alternate host.

Different host plants may affect the suitability of the insect host for its parasite. Dark-fired tobacco so conditions *Protoparce sexta* (Johan.) feeding upon it, that *Protoparce* becomes unsuitable for development of its parasite *Apanteles congregatus* (Say) (Gilmore, 1938). The California red scale parasite, *Habrolepis rouxi* Comp., develops successfully in red scale grown on citrus but not on red scale grown on *Cycas revoluta* (Flanders, 1940).

The parasite fauna of a given host often varies considerably in different areas, even between areas superficially similar. This merely emphasizes the rather narrow limits of adaptability that many parasites possess. Thompson & Parker (1928), following a detailed study of the parasites of *Pyrausta nubilalis* (Hbn.) in Europe, stated that "The variation in the composition of the fauna parasitic upon *P. nubilalis* in different zones is often considerable. Each zone has its characteristic group of parasites, differing both quantitatively and qualitatively from those of other zones. The existence of a species in a given zone depends on the variations in its limiting factors."

Many similar examples are known. In southern California, *Aphytis lingnanensis* Comp., is an efficient parasite of the California red scale in coastal citrus areas but not in interior citrus areas (DeBach *et al.*, 1955). In Nova Scotia *Aphytis mytilaspidis*

(LeB.) usually produces good natural control of the oyster-shell scale in the Annapolis Valley but not in Central New Brunswick (Lord & MacPhee, 1953).

Many of the parasitic fauna of citrus trees in southern California are limited in distribution or abundance in certain areas. This includes such important parasites as *Aphytis chrysomphali* (Mercet), *Comperiella bifasciata* How., and *Metaphycus helvolus* (Comp.). Inasmuch as these are all citrus-growing areas, it is evident that they do not vary greatly in weather conditions, but even so, certain parasites are adapted to some and not to others.

### OCCURRENCE OF ADAPTIVE RACES IN NATURE

Although most species of parasites seem to be rather restricted in their range of adaptability, certain ones have developed adaptive races.

An insight into the possibilities of artificially developing improved strains of parasites may be gained by a review of some known instances of naturally occurring parasite races. Such races may be "biological," "physiological," or "geographic" and may or may not be distinguished morphologically from the type of the species. Field races differing in biological characteristics or environmental adaptation, may, of course, be of considerable importance in importation and colonization programs. Clausen (1936) points out that "At one time it was assumed that a given species had a definite and fixed capacity in relation to its host and that this applied throughout its range of distribution. Recent work has demonstrated that this is not the case . . . Heretofore we have obtained our supply [of parasites] for importation from localities where large numbers could be more easily and cheaply secured. It now appears, however, that to secure the maximum results, each species must be studied throughout its range, and importations made from different regions, if there is reason to believe that a difference in habit or quality exists."

It is only when naturally occurring races are unknown, or show no advantages, that a program for artificial development of an adaptive race should logically be undertaken. Some cases of differences between races follow.

#### CLIMATIC ADAPTATION

Lund (1934), working with races of *Trichogramma minutum* Riley, found that the Louisiana gray race develops more slowly than the California yellow race at low temperatures and more rapidly at high temperatures. The mortality of the gray race was greater than that of the yellow race at low humidities and slightly less than that of the yellow race at higher humidities. Similar work of Flanders (1931) demonstrated that a yellow race from Massachusetts was less responsive to variations in temperature, had a shorter life cycle, and developed in a normal manner at a higher temperature than the dark race from tropical Mexico.

#### BIOLOGICAL ADAPTATION

Clausen (1936) states that studies on *Tiphia popilliavora* Roh., an introduced parasite of the Japanese beetle, have shown a marked difference in reproductive capacity between stock from Korea and that from Japan, and also an appreciable difference in the time of emergence. In this instance a late emerging form should be of much greater value because of the larger number of host grubs that are in proper stage for attack at the time the wasps are ready for oviposition.

Recently I have discovered what appears to be a race of *Metaphycus luteolus* (Timb.) in Mexico, which differs in important biological characteristics from the *M. luteolus* we know in California. They are indistinguishable morphologically. This species in California reproduces as a solitary parasite of the young stages of the black scale, *Saissetia oleae* (Bern.), and does not attack the larger scales, although it attacks all stages of the soft (brown) scale, *Coccus hesperidum* L., developing gregariously in the larger scales. In Mexico *M. luteolus* attacks all stages of the black scale and develops gregariously on the larger scales but has not been reared from soft (brown) scale. This solitary-gregarious development through all stages of black scale could be of considerable importance in biological control of this scale in California.

## HOST PREFERENCE ADAPTATION

Three species of diaspine scale parasites have been introduced into California, each of which has two races parasitic in different host species. Morphologically the races within each species are indistinguishable. *C. bifasciata* from Japan became successfully established on the yellow scale, *Aonidiella citrina* (Coq.), but not on the closely related California red scale, *Aonidiella aurantii* (Mask.). About 10 years later *C. bifasciata* imported from China became successfully established on the red scale.

In 1943, *Prospaltella perniciosi* Tower, parasitic on the San Jose scale, *Aspidiotus perniciosus* Comst., in Georgia, was introduced and became widely established on this scale in California. It was never taken on the California red scale. In 1949 California red scale imported from Formosa yielded *P. perniciosi*, which was then reared in large numbers on the red scale, colonized, and successfully established.

In 1948, a parasite, *Aspidiotiphagus citrinus* (Craw), present for many years in California as a parasite of oleander and yellow scales but not of red scale, was reared from red scale imported from China. This race was successfully cultured on red scale in the laboratory, whereas the race from the oleander or yellow scales could not be propagated on this host.

It is now well recognized that as Flanders (1950) stated: "The discovery that *C. bifasciata*, *P. perniciosi*, and *A. citrinus* consist of host-limited races finally establishes the principle that in parasite importation programs cognizance must be taken in this phenomenon. The host specificity of a parasitic species in one region is not necessarily the same as that in another."

Yasumatsu (1951) in Japan apparently discovered another case of change in host preference. The scale *Ceroplastes rubens* Mask. up to 1946 was a serious pest free from parasitization by *Anicetus ceroplastis* Ishii, which previously attacked only a related scale, *Ceroplastes ceriferus* And. In 1946 *A. ceroplastis* was found commonly attacking *C. rubens* in Kyushu. Yasumatsu considers this phenomenon to represent the development of a new race of *A. ceroplastis*, possibly due to a gene change arising by mutation. The new race has since been successfully spread throughout infested areas of Japan.

## FIELD EFFECTIVENESS

A race or strain of parasite species from one area may be generally more effective than that from other areas. For instance, the New Jersey strain of *Macrocentrus ancyli-vorus* Roh., a parasite of the oriental fruit moth, *Grapholitha molesta* (Busck), has been demonstrated to be the most effective one following colonization in many different states (Clausen, 1936).

*Aphytis maculicornis* (Masi), a widely distributed parasite of *Parlatoria oleae* (Colvée), has been found by Hafez & Doutt (1954), to consist of at least three biologically distinct strains. These strains (or "sibling species," since they are reproductively isolated) differ significantly in duration of developmental stages, sex-ratio, and number of progeny per female. Doutt (1954) has found the Persian strain to be much more effective than the other two in the field in California.

## TAXONOMIC RACES

The extent of occurrence of races or strains of parasites in nature might best be obtained from taxonomists. In most cases the more a genus or species is studied, the more apparent it becomes that great variation exists, often to the point of making it extremely difficult to draw distinctions between taxonomic units. The genus *Aphytis*, members of which usually attack diaspine scale insects, may serve as an illustration. Harold Compere, of the University of California at Riverside, has specialized in this group for many years and has an extensive world-wide collection. He finds, however, that the more specimens he acquires, the more difficult the problem becomes, because morphological gradation of taxonomic characters within and between species becomes virtually continuous. This in itself is evidence that races or strains must be commonplace.

## CONCEPTS OF SELECTIVE BREEDING

Selective breeding for better-adapted strains is just as logical for insect parasites as for domestic animals and cultivated plants. Marvelous changes beneficial to man



have been wrought. Selective breeding as an art and as a science is thoroughly established, but among entomologists has been practised mainly by apiculturists.

The concept of utilizing naturally occurring biological races or strains of parasites has been prevalent only since Clausen (1936) emphasized that parasite species do not necessarily have a definite and fixed capacity in relation to the host, which extends throughout the range of distribution. He suggested making importations from different regions if a difference in habit or quality of the parasite species was evident.

The concept of artificially developing an improved race or strain of parasites apparently was first suggested and tried by Wilkes (1942). He says "it seems probable that the methods utilized in this investigation . . . could be applied to other characteristics involved in the relations between parasite and host. The work of Thorpe and others has shown that the host preferences of parasites . . . are relatively plastic. Further analysis, combined with constructive breeding work on Mendelian lines, might allow us to duplicate in regard to parasites the results obtained with domestic animals and provide material far better adapted to the needs of the economic entomologist than that which Nature provides."

The principals of selective breeding have been thoroughly covered in many genetic and biological publications. Much of the previous work, including that with many insects, undoubtedly can be applied to insect parasites.

Fundamentally, there are four criteria or steps necessary in the successful development and use of an improved strain of parasite: (1) determination of characters needing improvement, (2) presence of or provision for adequate genetic variability in the stock to be selected, (3) adequate selection and breeding procedures, and (4) maintenance of integrity of the new strain in the field.

#### DETERMINATION OF CHARACTERS NEEDING IMPROVEMENT

It is evident from previous discussion that parasite species are frequently adapted to a narrow range of environmental conditions and that any departure from such conditions may limit their effectiveness. One way to surmount such weaknesses would be to develop, through selective breeding, adapted races. However, any or several of a multitude of causes may be responsible for poor adaptability; hence in order to plan a selective breeding program wisely, the exact nature of a parasite's lack of environmental adaptability must be known or determined. A detailed discussion of the varied means of obtaining such information is somewhat outside the scope of this paper. Suffice it to say that the answers, if not obvious, will be found in careful biological or ecological studies such as those previously cited, as well as in the two following illustrations.

Two recent papers have dealt with field cases of parasites which are intrinsically capable of satisfactorily controlling their host, but which fail to do so as a result of adverse effects of certain field environmental conditions. Lord & MacPhee (1953) found that the parasite *A. mytilaspidis* produced natural control of *Lepidosaphes ulmi* (L.) in the Annapolis Valley of Nova Scotia, which is characterized by relatively mild winters, but that the severe winters of central New Brunswick caused such mortality of the parasite that natural control did not occur. The general temperature differentials responsible for the observed differences in control were determined.

In California, DeBach, Fisher & Landi (1955) found that the parasite *A. lingnanensis* was capable of good biological control of the California red scale on citrus in coastal climatic areas but not in interior climatic areas. They found that low winter temperatures in the interior caused excessive mortality of the parasite in relation to the host and that high summer temperatures and low humidities were also detrimental, with the result that the parasite could not control the host. Temperatures and humidities causing excessive mortality were determined. As a result of these studies a program of selective breeding has been initiated in an attempt to develop a strain of *A. lingnanensis* capable of tolerating more extreme climatic conditions.

#### PROVISION FOR ADEQUATE GENETIC VARIABILITY

The successful development of an improved strain of parasite depends to a large degree upon the amount of genetic variability available in the stock undergoing



selection. In many cases imported parasites represent only a very small fragment of the natural population, not only in numbers but in distribution. Thus a stock imported from only one locality may represent a more or less pure line with distinctly limited possibilities for improvement through selection, and present as well the dangers often associated with inbreeding. It is likely that the oft-observed decline in inbred cultures of introduced parasites is the result of involuntary selection of an ill-adapted pure line (Simmonds, 1947).

It has been known since Johannsen's work early in this century that selection is effective in genetically mixed populations but inoperative in genetically uniform ones. Thus the pool of genetic variability available in the stock to be selected should be enhanced by acquisition of as many individuals from as many points of the parasites' geographic range as is practicable. For instance, selection for a quantitative character may fail to modify the character further, but if the selected strain is crossed with a similar one from another source, selection among the progeny often successfully modifies the character considerably. This would occur if the first race contained only a limited number of genes for the character in question, and when these had become homozygous as a result of selection, no further change was possible. The introduction of different genes belonging to a series of multiple factors determining this character would make it possible to obtain a stock with a larger number of genes and thus to establish the character on a permanently higher level.

Additional genetic variability may be introduced or at least speeded up through irradiation procedures. Irradiation produces gene mutations, gross mechanical changes involving rearrangement of the genic material within the chromosomes and reduplication or losses of whole chromosome sets.

The desirable amount of radiation or "r" dosage varies considerably between species. It must be determined experimentally for any particular species by tests varying dosages and/or exposure time. Excessive irradiation can produce such drastic chromosomal changes in eggs or sperm that complete inviability will result. Practical aspects of a breeding program require that progeny production by irradiated females remain at a fairly high level in order to maintain cultures. A good working hypothesis might well limit the "r" dosage level to that not reducing progeny production more than 25-50%, thus insuring a minimum of lethal chromosomal changes caused by irradiation. In current irradiation tests with *A. lingnanensis* we have determined that 550 "r" units represent about the maximum dosage compatible with maintenance of adequate culture population levels.

Another source of genetic variability lies in making interspecific crosses. The probability of such crossing is slight, especially in nature, but the chances may be substantially increased in the laboratory through proper manipulation. We have greatly increased the rate of copulation between species of *Aphytis* by CO<sub>2</sub> anesthetization before placing the sexes of different species together. We are now working on a method of eliminating all the barriers to successful cross-species fertilization in *Aphytis* up to the time of actual penetration of the sperm into the egg. This will involve removal of mature haploid eggs from the ovaries of species "A", removal of sperm from spermathecae of species "B" (more practical than removing sperm from testes of male), placing them together in a suitable medium, then placing the presumably fertilized egg upon the host scale for development. Half the process has been successfully worked out. Mature haploid eggs have been removed from the female of *A. lingnanensis*, transplanted to the host scale, and reared through to the adult male. The removal of sperm and its maintenance in a viable condition in a suitable medium needs to be worked out before species crosses can be tried by this method.

Sailer (1954), after successful interspecific crosses with stink bugs, concluded that "In view of the number of successful crosses in *Drosophila*, Culicidae, Lepidoptera, Pentatomidae, we should begin to think of hybridization as a means of breeding new and superior strains of parasites and predators. No doubt some progress in this direction could be made through selection within species, but hybridization can make it possible to introduce a desirable character from one species into another so that an ill-adapted parasite or predator may become a more efficient agent in the control of a pest species."

## SELECTION PROCEDURES

Selection procedures will vary with the organism involved and in many cases will be dictated by practical rather than theoretical considerations. We may wish to achieve rapid results by drastic selection, eliminating, say, 99% of the progeny in each generation. The feasibility of such a process will depend upon the reproductive capacity of the species, that is, upon the ability to maintain desirable population levels of the cultures, and upon the type of inheritance involved. If we are selecting for a character influenced by many different genes, rigorous selection may eliminate certain of these genes early and reduce the chances of obtaining the best ultimate combination. On the other hand, a low selection rate may require such an extreme number of generations to produce results that the program will be impractical.

Good procedure might involve use of the highest selection rate consistent with maintenance of high culture population levels. In cases where only one to several genes are determining the character in question, selection could be more rigorous and culture populations could be lower. However, the effectiveness of selection may be very low in small populations (Dobzhansky, 1937, p. 182). In attempts to develop a low-temperature-tolerant strain of *Aphytis* in California, we subject 10,000 to 20,000 individuals to temperature selection each generation. Mortality must not exceed about 50% or culture population levels cannot be maintained. This procedure is based on the hypothesis that polygenic inheritance is involved.

It must always be borne in mind that in modifying one character favorably others may go in the opposite direction. The ultimate results will become apparent in the field, but at intervals suitable laboratory tests should be made to check such factors as sex ratios, rate of development, and survival to other conditions.

## MAINTENANCE OF INTEGRITY OF NEW STRAINS

There is little practical purpose in selecting an adapted strain if upon field colonization it proceeds to cross with unadapted individuals of the same species. Normally the program would not be undertaken if this possibility existed, but there may be cases where the parasite species maintains itself in the field in fair numbers but not sufficient to exert successful control. Colonization of a new strain under this condition would necessitate the development of some sort of genetic isolation between the strains previous to colonization of the improved strain.

The most satisfactory way to obtain genetic isolation would be to select a parthenogenetic uniparental strain of the adapted strain. Races of parasites producing only females are of fairly frequent occurrence in several groups of parasites. Development of a uniparental strain would involve isolation of large numbers of virgin females and selection of those, if any, which produced female progeny.

The development of other types of reproductive isolation would doubtless be much more difficult and would in nearly all cases depend upon further selection of the adapted strain. This might be more difficult to obtain than the originally sought adaptation. Isolating mechanisms are extremely diversified. They include failure to interbreed because of differences in habitat, differences in breeding seasons, lack of attraction between sexes, physical difficulties in copulation, and physiological failure of fertilization or development of the fertilized egg or embryo.

## RESULTS OF SELECTIVE BREEDING

Selective breeding of parasites has already achieved some very interesting results. Most of this work, however, has been limited to laboratory application.

Wilkes (1942) appears to have been the first to select a strain of parasites artificially. Working with *Dahlbominus (Microplectron) fuscipennis* (Zett.), a parasite of the European spruce sawfly, *Diprion hercyniae* (Htg.), he endeavored to select a strain which might show greater adaptability in cooler field locations where success of the parasite had been noticeably limited. By means of a temperature gradient it was found that in a large random-breeding population, a temperature-gradient response curve showed two principal groups congregating at temperatures around 8° and 25°C., with a lesser peak at 15°C. Selection of individuals congregating in the 6°-10°C. zone resulted, within four generations, in the development of a strain in which over 50%

of the adults preferred temperatures below 12.5°C. This represents an almost complete reversal of the normal curve for the original laboratory stock.

Further studies were made (Wilkes, 1942) comparing the low-temperature preference of the selected laboratory strain with that of individuals recovered from a field area having a low mean temperature. Both strains showed nearly identical low-temperature preferences. Such results might be expected, inasmuch as natural selection in the field was operating in much the same manner as artificial selection in the laboratory and parental stocks were from the same original source. The very rapidly developed adaptation in this case might indicate a simple type of inheritance. Practical application seems limited, inasmuch as further selection did not appreciably lower the temperature preferendum and the field-selected strain still remained rather ineffective in control of the host. Further progress would seem to depend upon the introduction of additional genetic variability into the stock, but the importance of the results in pointing out possibilities in temperature adaptation of parasites is not diminished.

Improvement of seriously declining sex ratios in laboratory parasite cultures was obtained by Simmonds (1947) and Wilkes (1947) through selective breeding procedures. The proportion of males in these stocks was becoming so great that cultures were in danger of being lost. Wilkes showed that continued inbreeding in laboratory cultures was responsible for the prevalence of male sterility, which resulted in decreased proportions of females in successive generations. By outbreeding and selection for high female production he found that the percentage of sterile males could be drastically reduced. He was also able to increase the mean number of progeny per female from 34 to 68, and to improve oviposition and longevity. The result was a tremendous increase in the efficiency of mass production of *Dahlbominus* for field release.

Simmonds through selective breeding between families showing high proportions of females was able to increase the sex ratio favorably. These results were interpreted as being due to the breeding out of factors inducing male sterility. The efficiency of mass rearing of parasites was greatly increased as a result of the selective breeding.

Through selective breeding Allen (1954) achieved some extremely significant results in the modification of host preference of a parasite. This work opens a wide vista for similar work with other parasites. Initially, Allen had to use attractants to "persuade" the Oriental fruit moth parasite, *Horogenes*, to oviposit in a foster host, the potato tuberworm *Gnorimoschema operculella* (Zell.). After about 11 generations of rearing the parasites on the tuberworm under this process, it was found that a strain had been segregated which no longer required an artificial stimulus to induce oviposition on the foster host. Further segregation for 39 generations resulted in a strain which propagated 24 times as efficiently as the original on the potato tuberworm. The artificial selection of strains of parasites having changed host preferences could have great practical importance in the field aspects of biological control. Starting, for instance, with a parasite which effects good biological control of its host in the field, if a change in host preference to another related pest could be induced, then biological control of the other pest might likewise be obtained. It has already been pointed out that such races or strains of parasites occur in nature.

Another important possibility for selective breeding lies in the development of strains of parasites resistant to the adverse effects of insecticides. Pielou & Glasser (1952) were able to increase the tolerance of *M. ancyliivorous* to DDT by several times following nine months of selection. This phenomenon is similar to the numerous instances of the development of resistance to DDT by houseflies and other insects. It is to be expected that *Macrocentrus* might develop, through natural selection, a degree of resistance in the field similar to that obtained in the laboratory, inasmuch as laboratory and field parasite stocks were presumably from the same original source. The addition of more genetic variability, as through the acquisition of additional stocks from other geographic locations than the original stock might permit the development of an even greater level of DDT tolerance through selection.

Another attempt to improve a parasite through selective breeding along other lines was performed by Urquijo (1951) with *T. minutum*. He selected strains for ovotropism

(host-finding ability) and was able to increase this ability fivefold in three years. Field tests with this strain appeared to give improved results.

### GENERAL DISCUSSION

The big question which might arise from any discussion on the practicability of selective breeding would be "Can selective breeding accomplish what natural selection in the field would not do anyway?" A single answer would not suffice, but it could be "No," if haphazard, unplanned selection were followed.

On the other hand, laboratory manipulation can duplicate and greatly speed up events which occur rarely in the field. Genetic variability in the stock to be selected can in some cases be increased considerably beyond that which might ever be obtained under natural conditions. This, of course, is the key to the successful development of a better-adapted strain.

Laboratory manipulation can even produce results which might never occur under field conditions. For instance, most species possess a certain tolerance to seasonal changes. Dobzhansky has shown that the genetic equilibrium of insect populations change as seasons change, that is, winters result in certain adaptive changes, summers in others. Summer adaptation may, however, develop at the expense of winter adaptation, so that at the end of one season the population is ill adapted to the following season. This could be because in nature *individuals of a given population* are not subjected to both winter and summer conditions. Natural selection of *individuals* having a wide range of temperature tolerance would therefore be unlikely to occur. In the laboratory both winter and summer conditions can be applied against the same population; hence the probability of artificially selecting a better-adapted strain should be greatly increased. Other manipulations which produce in the laboratory conditions rarely or never occurring in the field can doubtless be applied to the development of better-adapted strains.

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### DISCUSSION

A. P. KAPUR. I should like to know of some concrete examples of predatory insects in which improved strains have been selected and stocks maintained of such strains successfully.



PAUL DEBACH. Host preference in *Chrysopa* have been changed. Improved strains of coccinellids have been developed.

A. D. HINCKLEY. Do not insect populations sometimes become resistant to two unrelated insecticides applied at different times? Is this not comparable to the effects of heat and cold on insect populations?

PAUL DEBACH. Yes they do; however, all known cases of selection of insects, with respect to one temperature, have resulted in adaptation in one direction only. I feel that *individuals* must be selected for resistance to both high and low temperatures.

F. J. SIMMONDS. Selection of definite strains in the laboratory may not be very successful owing to other detrimental effects produced. Better to obtain material of maximum genetical variability and liberate this and allow the environment to select the best of these genetical components.

PAUL DEBACH. This may be true; however, it may be possible to carry out types of selection in the laboratory, which rarely or never occur in nature and thus develop strains which would not occur naturally. This point is discussed in my paper.

J. G. ROBERTSON. It is difficult to concede that interspecific hybridization will yield characters in insects that may be of significance in biological control. The loss of fecundity, viability and number of progeny, under such hybridization, are, in fact, used as taxonomic criteria.

PAUL DEBACH. If viable progeny are obtained, which produce, which admittedly would be extremely rare, then viability in the hybrids would be increased over parental stocks and subsequent selection might well result in adaptations in the desired direction.

S. E. FLANDERS. The work of Whiting and Schmieder with *Habrobracon* and *Melittobia* indicates that the cross-breeding of hymenopterous species of parasites is difficult, if not impossible. In the continuous mass cultures of parasitic Hymenoptera inbreeding does not appear to be detrimental. Deterioration of cultures is usually, if not always, caused by other factors. The rearing of parasites from field-collected hosts does not mean that on such hosts the parasites have reproduced more than the reared generations.



# Adaptability of Entomophagous Insects to Environmental Changes

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## ABSTRACT

The tachinid parasite *Drino bohémica* Mesn. is able to adapt itself to changes in the availability of different hosts. Though in the field it most frequently attacks *Diprion hercyniae* (Htg.), it has degrees of preference for other species of Tenthredinidae and may attack them even in the presence of *D. hercyniae*. It has degrees of preference for stimuli from the food trees of different hosts. These stimuli initiate searching behaviour as strongly as do those from white spruce, the preferred food tree of *D. hercyniae*.

Four lines of the parasite were developed (Monteith, 1955, *Canadian Ent.* 87: 509-530) to determine if the preferences of the parasite could be changed. The degree of preference by parasites from each of these lines for the host on which they were bred increased, but only temporarily. The line that was bred on *Neodiprion lecontei* (Fitch) was studied for 28 generations. The degree of preference for *N. lecontei* fluctuated continuously and appeared to change through a complete cycle.

The line bred on *N. lecontei* has been reared for many more generations, and preferences of parasites from the F71 - F83 have been tested. The degree of preference for *N. lecontei*, and for other hosts included in the study, has continued to change. These changes amplify the observations made by Monteith (1955, *ibid.*).

Changes in the degree of preference by *D. bohémica* for different hosts were found, but none of these changes were fixed after 80 generations and physiological races were not obtained.

The changes, and the fluctuations, in the preferences of this parasite indicate an adaptiveness to environmental changes superior to that permitted by the development of fixed racial habits. The role of the changes in determining host preferences and the importance of preimaginal conditioning in *D. bohémica* was discussed.

A full report of this study will be published elsewhere.



# An Interesting Case of Biological Control of *Ceroplastes rubens* Maskell in Japan

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## ABSTRACT

Since the introduction of *Ceroplastes rubens* Maskell into Japan in 1897, it has been an important pest of various economic plants (citrus, persimmon, tea, etc.). The introduction of its parasites from Hawaii and California was attempted during 1932 to 1938, but without success.

In 1946 the author discovered an effective parasite (*Anicetus beneficus* Ishii et Yasumatsu, 1954) of this scale in Kyushu, in the southern part of Japan. Since 1948, large numbers have been liberated in various orchards on the islands of Honshu and Shikoku and commercial control of the scale was achieved within three or four host generations after release.

The possibility is suggested that this parasite may have evolved from *Anicetus ceroplastis* Ishii by mutation in relatively recent years.

Since the introduction of *Ceroplastes rubens* Maskell into Japan in 1897, it has been an important pest of various economic plants (citrus, persimmon, tea, etc., more than 150 species of plants being attacked in Japan). The introduction of its parasites (*Aneristus ceroplastae* Howard, *Microterys kotinskyi* (Fullaway), *Moranila* (= *Tomocera*) *californica* (Howard) and *Scutellista cyanea* Motschulsky) from Hawaii and California was attempted during 1932 to 1938, but without success. Chemical methods were, therefore, adopted as the only possible method of control, though the horticulturists anticipated some injury to economic plants and encountered some difficulties in the effective control of this scale by the applications of insecticides.

In 1946, the author had the good fortune to discover an effective parasite (*Anicetus beneficus* Ishii et Yasumatsu) of this scale in Kyushu, in the southern part of Japan. Since 1948, large numbers of this parasite have been liberated in various orchards on the islands of Honshu and Shikoku of Japan for the control of this scale (1-3, 5-6, 10-19, 21, 27, 29, 30). The author's field investigations covering eight years in various orchards reveal that definite commercial control of the scale has been achieved within three or four host generations after release. In no case have the liberated parasites failed to establish themselves in new habitats in Honshu and Shikoku (1, 6, 11, 13, 15, 18, 21, 39). The effectiveness of this parasite is satisfactorily indicated in the case of one village in Shikoku where the damage caused by this scale was extremely severe. The village had 4 acres of Citrus orchards (approximately 3000 Citrus trees), and three years after one release of 20 female individuals of *A. beneficus*, it became almost impossible to find any scale insects in the orchards. According to the author's estimate almost all the scales infesting 100 Citrus trees would be completely controlled within three or four years after the release of one fertilized female parasite.

*A. beneficus* Ishii et Yasumatsu has two generations a year. The adults of the first generation start emerging late in May and continue to emerge until early in July. Emergence of the second generation begins the middle of August and continues until the middle of October. On the other hand the host scale, *C. rubens*, has but one generation a year. The author's experiments show that the parasite oviposits in scales in almost any stage of development except the youngest one which is still uncovered by wax and the oldest one which has finished oviposition. In Japan oviposition of the adult scales and the hatching of the young individuals take place continuously from about the middle of May to August, a period of about three months or more. This irregularity of oviposition or growth on the part of the host scales appears to demonstrate one of the main reasons for the success of the parasite in maintaining itself during the early summer (2-4, 10, 19, 29-35, 40). The female of this parasite has the power of oösortion, and the longevity of the parasites seems to be sufficient to enable them to bridge the gap between their emergence and the occurrence of scales that are old

enough for oviposition. The parasite finds food very easily, because its food consists of honeydew secreted by its host scale and by Aphids. The average number of eggs deposited per female per day is about 5, and one female may deposit more than 500 eggs under favorable field conditions. The reproduction is bisexual; the sex ratio is 0.5. virgin females produce male progeny (arrhenotokous parthenogenesis). Under favorable field conditions the adult parasite, irrespective of its sex, can survive for two or three months. This parasite has the ability to avoid detrimental environmental conditions such as a heavy rainstorm or spraying of insecticides. Under such conditions the parasite comes to rest on the underside of leaves or other places where it will be protected. Normal activity of this parasite was found to take place below 25°C (37). The female seems to be somewhat sluggish in behavior, but can disperse gradually as it attacks the host scales. One example from the author's investigations indicates that a population of this parasite may disperse a distance of 2000 meters within two years (34, 39). Thus, when liberating this parasite in the field it is recommended that small numbers of individuals be released here and there, in several different places, to increase the effectiveness of the parasite. The physiological differences, if any, among the scale insects feeding on different host plants are not known to affect the ability of this parasite at all. *A. beneficus* reared from *C. rubens* on various host plants may be used indiscriminately in liberations against the scales (38).

Fortunately this parasite has no known secondary parasites (31, 34). Only one parasite larva matures in a host, even in the case of superparasitism. The full-grown larva excretes its meconium just before pupation. The meconium is deep black in color and is smeared by the larva on the inner side of the body of the host. When dried, the black, thin and fragile film of larval meconium can easily be seen through the wax covering of the scale. If this wax is knocked off by the wind or rain, this thin and very shining meconium-covering will remain adhering to the host plant. Thus the establishment of *A. beneficus* in a district is easily detected by the characteristic dark color of the meconia of the parasites. There will also be one exit hole of the adult parasite through the body wall and the wax covering of each parasitized scale. This exit hole is always found on one side, along the longitudinal axis of the scale. The larva of the second generation of this parasite overwinters in the host scale in the full-grown larval stage, and pupation does not occur until the middle of the next April in Kyushu, Honshu, or Shikoku (4, 19, 34, 35).

As far as our investigations go, three species of *Anicetus* occur in Japan.

1. *Anicetus annulatus* Timberlake  
Distribution: Japan (Honshu, Shikoku and Kyushu), California and Hawaii (introduced by chance many years ago).  
Hosts: *Coccus hesperidum* Linné. *Coccus pseudomagnoliarum* Kuwana, *Eucalymnatus tessellatus* Signoret, *Pulvinaria aurantii* Cockerell, *Pulvinaria* spp., *Saissetia hemisphaerica* Targioni-Tozzetti, etc.
2. *Anicetus ceroplastis* Ishii  
Distribution: Japan (Honshu, Shikoku and Kyushu).  
Host: *Ceroplastes pseudoceriferus* Green.
3. *Anicetus beneficus* Ishii and Yasumatsu  
Distribution: Japan (Kyushu, introduced from Kyushu to Honshu and Shikoku).  
Host: *Ceroplastes rubens* Maskell.

Three species of *Ceroplastes* occur in Japan; viz., *japonicus* Green, *pseudoceriferus* Green and *rubens* Maskell, but not a single species of *Anicetus* attacks *Ceroplastes japonicus*. Among the three species, *annulatus* is quite different from *ceroplastis* and *beneficus* in many characters (32). But it is extremely difficult to distinguish *A. ceroplastis* and *A. beneficus* with the naked eye or even with a low power binocular microscope. For several years *A. beneficus* was considered to be a Kyushu race of *A. ceroplastis* (32). Comparative morphological studies reveal that *A. beneficus* is much closer to *A. ceroplastis* than to any other members of the genus (9, 25, 32). Silvestri

and Gressitt made extensive surveys of the parasites and predators of Citrus pests in various districts of China, but could not find even a single effective parasite of *C. rubens* (30, 32). Several species of *Anicetus* from China in the collection of the Department of Biological Control, University of California, differ entirely from *A. beneficus*. Further, a world revision of the genus *Anicetus* is now underway by Compere and the author jointly, but the material of *A. beneficus* at present available is all from Japan. According to most of the Chinese literature on Citrus pests, *C. rubens* still remains as a troublesome pest in that country.

Since the introduction of *C. rubens* probably from China (first found in 1897 at Nagasaki, Kyushu), it is scarcely conceivable that additional introductions of such a noted pest from foreign countries would have occurred, because the plant quarantine system of inspection of imported trees was vigorously enforced by the Japanese Government up to 1945. According to the author's opinion, *A. beneficus* might have begun its activity around 1942 in Kyushu. If *A. beneficus* had been introduced into Kyushu by chance from an unknown foreign country, we should expect to be able to find a center where the parasites first established themselves and from which the population of both the parasite and host decreased somewhat concentrically outwards. Notwithstanding, the author's investigation supports the fact that more than one ancestor of *A. beneficus* might have arisen at practically the same time at different foci through Kyushu, because it is hardly possible to consider that spread of this parasite would have occurred from a single focus (31). If the parasite is of foreign origin, the species should have been discovered somewhere in the world many years before the supposed introduction into Japan, because the recognition of the parasitized scale is quite easy in the case of this parasite and the effectiveness of the parasite is quite outstanding.

Fluctuation in the populations of *C. rubens* is often influenced by such characters as climate, tree and some cultural conditions. During World War II almost all the orchards in Japan were neglected, and the fruit trees received little or no attention for a considerable period. There has been no noticeable difference in climate on Honshu, Shikoku and Kyushu where scales have had no insecticidal control during these years. Nevertheless, only in Kyushu has the population of *C. rubens* been reduced noticeably in recent years. Field surveys proved that *C. rubens* in Honshu and Shikoku were entirely free from the parasitization by *A. beneficus* and the progressive decrease in the population of *C. rubens* in Kyushu was due to the activity or existence of the key parasite, *A. beneficus* (32). On the other hand its closest relative, *A. ceroplastis*, occurs in Honshu, Shikoku and Kyushu, parasitizing *C. pseudoceriferus*.

The relation of females of *A. beneficus* and *A. ceroplastis* to *C. rubens* and *C. pseudoceriferus* is of interest. When placed with *C. rubens* and *C. pseudoceriferus*, the females of *A. ceroplastis* oviposit exclusively in *C. pseudoceriferus* and pay no attention to *C. rubens*, while the females of *A. beneficus* prefer to oviposit in *C. rubens*, but sometimes oviposit also in *C. pseudoceriferus*, although nothing is known about the mortality of the progeny in this case (22, 26). Many scale insects other than *C. rubens* have been studied with special reference to their natural enemies, but *A. beneficus* has been reared exclusively from *C. rubens*.

The males of *A. ceroplastis* pursue the females of *A. beneficus*, and the males of *A. beneficus* also pursue the females of *A. ceroplastis*, although copulation has never been observed between the species. The females of *A. ceroplastis* show no interest in the males of *A. beneficus* (26).

Though the sudden appearance of an effective parasite of *C. rubens* in Kyushu, Japan, about 1942 is a mystery, the evidence discussed above strongly suggests the possibility that *A. beneficus* may have evolved from *A. ceroplastis* by mutation in relatively recent years. Unfortunately, the author knows of no other similar occurrence in the history of the biological control of insect pests. Of course it is too early to derive such a bold conclusion about the nature of *A. beneficus*. More extensive surveys of the natural enemies of *C. rubens* should be done on a world-wide scale, and some cytological and genetic study is also needed between *A. beneficus* and *A. ceroplastis*. Experimental studies in attempting to produce some mutants from *A. ceroplastis* by certain artificial methods are also desirable.



The author holds the opinion, however, that the problem of *A. beneficus*, an effective parasite of *C. rubens*, may offer an interesting thesis to scientists from the standpoints of agricultural and evolutionary science.

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# An Analysis of the Balsam Woolly Aphid Problem in Europe

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## ABSTRACT

*A review is given of the work done to date since 1950 by the European Laboratory, Commonwealth Institute of Biological Control, on *Adelges piceae* and *A. nüsslini* in Europe, a project assigned to it by the Canadian Government. Mere shipment of field collections was soon found unsuitable, while biocenotic studies on the *Adelges*, their host plant, community of predators, parasites and diseases were considered indispensable previous to any transfer of living material to Canada. The present paper gives the general plan of work followed by the European Laboratory, the different steps materialized, and concentrates mostly on the population dynamics inside the *Adelges* biocenosis, intending to give a preliminary picture of the outbreaks based on the findings obtained to-date. The role played by predators is emphasized and considered rather limited in Europe.*

Starting in 1950 on this project, in Switzerland and Southern Germany, we tried at first the usual method of field collection of predators, some rearings and immediate shipment of our material to Belleville, Canada. This was soon considered unsuitable in this particular case, by us as well as by our Canadian colleagues. Shipping these predators for release was considered dangerous because of the presence of their parasites and diseases, and also by possible competition or direct interaction between them. Moreover, the direct destruction of the *Adelges* eggs by these predators was certainly evident and even measurable, but their actual effectiveness was totally unknown. It was decided that more careful studies on the *Adelges* complex be undertaken by us in Europe, previous to, or at the same time as our first shipments. A better ecological understanding of this *Adelges* biocenosis was quite necessary, not only to make an intelligent choice between the predators, to eliminate their parasites, clarify their life-history, but also to help by comparison to estimate the results in Canada at the end of the project.

The problem appeared at first sight difficult and complex. The outbreaks of *Adelges* on the trunk of the European fir trees evidenced some remarkable facts. These outbreaks appeared on some groups of trees only, increasing and decreasing in the course of 2-3 years, then reappearing in other places, while almost all the trees of the forest were infested at a very low level, not developing outbreaks. Inside these outbreaks, the offspring of the aphid evidenced a very heavy mortality by overcrowding, loss in dispersion and lack of fixation, while a rich complex of predators, their parasites and diseases seemed to pick out of this living mass their own subsistence.

Facing all these facts, the general planning of our European work was started according to the classical method used in biocenotics, as it is explained for instance in Dr. Schwenke's papers:—

1. Mapping and limiting the *Adelges* biocenosis in Europe, choosing with the help of climatic and plant association documents the most suitable places having many similarities with the infested areas in Canada.

2. Analysis of the *Adelges* biocenosis, including all the natural enemies involved, their different instars and their complete life-history.

3. Study of the correlations inside the *Adelges* biocenosis or merocenosis.

4. Experimental researches on the population dynamics inside these *Adelges* biocenosis, including the discovery of the main factors involved, their action and interaction, trying to get a comprehensive understanding of the processes.

Shipping and release of the predators in Canada took place on a large scale toward the end of our studies mentioned under point 3. We were able, in most cases,

to ship predators free of parasites, by suitable rearings, convenient timing of collection, or selection of the suitable stage.

As to points 1, 2 and 3, I recall here the findings published by the staff of the European laboratory:—

Point 1. Climatic and biocenotic aspects of the collection of predators of *Adelges piceae* in Europe, by H. Pschorn-Walcher. (*Proc. Tenth Int. Cong. of Ent.*).

Points 2 & 3. V. Delucchi: *Pullus impexus* Muls. a predator of *Adelges piceae* Ratz. with notes on its parasites: *Bull. Ent. Res.* 45: 243-278. J. Franz: Same work on *Laricobius erichsoni* Rosenh. (in course of publication). V. Delucchi: *Aphidecta oblitterata* L. a predator of *Dreyfusia piceae* Ratz.: *Pflanzenschutzberichte* II: 73:83. V. Delucchi & H. Pschorn-Walcher: *Cremifania nigrocellulata* Cz. ein Räuber an *Dreyfusia piceae* Ratz. *Zeitschr. f. angew. Entom.* 36:107. V. Delucchi & H. Pschorn-Walcher: Les espèces du genre *Cnemodon* Egger prédatrices de *Dreyfusia piceae* Ratz.: *Zeitschr. f. angew. Entom.* 37: 492-506. Several unpublished reports on the other predators.

I will now deal with the 4th point, concerning the dynamics of the population inside the biocenosis, discussing the different results obtained to date, and giving a preliminary picture of the development of the outbreaks.

In Europe, *Adelges piceae typica* is evidenced on the trunk of almost each fir tree, localized around the lenticels of the bark, at a very low rate called by Pschorn & Zwölfer "the normal endemic density". This endemic density is lower in *Abietetum-fagetum*, higher in pure and dense stands of artificial fir forests.

At a certain time, the density of the aphids increases on the trunk of some groups of trees inside the forests, and outbreaks start. Periodical photographs and observations made on the infested trees showed always or nearly so the same type of gradation: progressively a high density is reached, even frequently overcrowding. The predator complex appears, then takes place a rapid decrease. The infestation shows a tendency to spread a bit on the trunk above and below the primary outbreak, then all disappears and the normal endemic density takes place again. All together, each outbreak lasts approximately 2-3 years (4-6 generations of *Adelges*).

The first question which arises is why are the aphids maintained so regularly and constantly at the normal endemic density during many years, and why are they developing outbreaks on a few trees only. A second question is why do the outbreaks develop so regularly in the same way of gradation (progradation and retrogradation) in the course of 2-3 years.

We have started studying the second question first, expecting that our knowledge on the gradations would help us to approach the first one. We must now take the opportunity to express our gratitude to W. Kloft, Plant physiologist at the University of Würzburg (Germany) who assumed an important part in these difficult researches.

First of all, it was observed that the number of eggs laid by *Adelges* females inside an outbreak was approximately twice the number of eggs laid by scattered specimens on trees with the normal endemic density. This was not due to the existence of two different strains of aphids since we have obtained regularly artificial outbreaks in our cages, starting on *Adelges* at the normal endemic density. This showed that the areas of heavily infested bark are, at least at the beginning of the infestation, more favourable to the development of the aphids, the result being an increment of their fecundity. Simultaneously, a satisfactory explanation of this fact was given by Kloft, who proved that the action of the *Adelges* develops the vitality of the bark, increases mostly its protein content, and creates what he calls a "physiological gall" not visible externally but well characterized by some reactions. This physiological gall is thus more suitable for the settlement of the crawlers of the following generation of *Adelges* and their density increases. At this stage, the outbreak is automatically self-accelerating.

Simultaneously, experiments were made to show which minimal density of *Adelges* was necessary at the beginning, to create a physiological gall. Artificial outbreaks were successfully developed on different trees bearing only the normal endemic density, in forcing a sufficient number of crawlers to settle inside cages. This suggested that



apparently all the trees may be infested provided the infestation starts with a certain minimal density.

What happens in these outbreaks is that the density increases generally until the bark is, in the infested area, completely covered by *Adelges*. A heavy mortality occurs in the course of the development of these aphids which require more and more space as long as they grow. The adults lay a huge number of eggs, of which approximately half are eaten off by predators (according to Franz and Wichman), the rest gives a flow of crawlers, of which an extremely small proportion is able to settle and develop successfully, because of overcrowding, insufficient dispersal, and accidents of all kinds. At this time, it seems that the predators, unless numerous and active, are quite ineffective.

However, at a certain time, the infestation breaks down. Kloft gives us an explanation of this fact: the phelloderm of the bark becomes exhausted, the cells die and are no more suitable to the multiplication of the *Adelges*. Moreover, the aphids degenerate. When removed from the decreasing outbreak, their crawlers do not settle as well as the others on fresh trees. Then, the area of bark bearing the outbreaks cleans up progressively, while a certain concentration of *Adelges* appears above and below on the trunk, soon reduced also by the same factors. The predators become proportionately more and more numerous; it may be that in some cases they are able to lower the density of *Adelges*, thus preventing the rapid exhaustion of the bark, and maintaining the infestation a little longer. Finally, they concentrate on the last degenerated aphids and eradicate the outbreak, preventing perhaps its propagation to other trees to a small extent.

As shown by Kloft, the bark recovers, exfoliating the destroyed phelloderm, regenerating new layers, and becoming again suitable for a new infestation after 2-3 years.

We are now in a better position to face the first question mentioned above: Why are the *Adelges* generally maintained in nature so regularly and constantly at the very low endemic density, and why are they developing outbreaks so scarcely, on a few trees only, and even not in all types of forests?

In fact, how do the *Adelges* pass in some cases from the normal endemic density, up to the minimal density necessary to start a physiological gall and a self-accelerating outbreak. Unfortunately up to the present stage of our investigations, no definite answer can be given to this question. However, we may say the following: this should not be due to sudden changes in the *Adelges* itself. As mentioned above, we obtained outbreaks artificially, starting from material at the normal endemic density. Then, it should be caused either by changes in the physiology of the trees, or by accidental reduction in some places of the normal action of specific or non specific predators, or either by accidental concentration of crawlers on a small area of bark, thus reaching the minimal density necessary to start a physiological gall.

Further researches should be undertaken along these lines during the coming years, to solve this difficult matter. We recommend for this, to use the ordinary method followed in biocenotics, consisting in experimentation made in nature. Some trees, similar to each other, should be partly put into cages, infested by *Adelges* at the normal endemic density, with or without predators, and then induced to produce outbreaks by some physiological changes of the trees as suggested by Kloft. Of course, we must not forget that climatic factors, at least by their extremes, play a role on the *Adelges*, trees and predators. Some of these experiments have already been started at Feldmeilen and we hope that they will bring us in the coming years some facts of interest. In order to be significant, such experiments must be made on a rather large scale, and repeated a good number of times.

Finally, we expect that our present communication, summarizing the status of the balsam woolly aphid problem in Europe, will help in understanding the interest of the following papers on the same subject, and show the position of each of them inside the general plan of researches established since several years.



# The Effectiveness of Predators and Food in Limiting Gradations of *Adelges (Dreyfusia) piceae* (Ratz.) in Europe

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## ABSTRACT

By mechanical-chemical exclusion of predators from parts of the bark of fir trees (*Abies alba*) infested with *Adelges (Dreyfusia) piceae* (Ratz.) it was possible to evaluate quantitatively the efficiency of predators in comparison to unprotected parts. A new method of recording was applied in which each single aphid was observed from insertion to death and registered on a special indexing sheet using a five-fold pantograph.

Very high mortality of the chermesids resulted from the activity of native predators mainly in the spring generation, according to meteorological conditions also in the autumnal generations, and leading sometimes to an end of the gradation of a single tree or in a local infestation. The second reason for the reduction of outbreaks is the damage done to the bark after heavy infestation of several years. The phellogen and phelloderm cells degenerate thereby preventing a permanent infestation.

In order to evaluate the effectiveness of both mortality factors (predators and exhaustion of bark) they were separated experimentally. Test zones of predator free bark were well infested for one year following the disappearance of the chermesid population on the rest of the stem. After this time, also the protected population declined. Simultaneously, a secondary phellogen appeared in deeper layers of the bark. Thus, both mortality factors are effective independently; the second one causes the reduction of the chermesids later and slower than the first one. Both factors together with other influences of more restricted importance secure the termination of an outbreak after a few years of heavy infestation.

In Europe, the balsam woolly aphid *Adelges (Dreyfusia) piceae* (Ratz.) lives mostly on the stems of maturing fir trees (*Abies alba*). Thus, in using the name "balsam woolly aphid" it must be kept in mind that the native host tree is not balsam fir, but European fir. On stems of the European fir this aphid does scarcely any harm. Damage to young fir trees which has been observed occasionally will not be considered in the present report. Mass outbreaks on stems of older trees usually disappear two to four years after being recognized. Reasons for the fluctuations were previously unknown.

Stimulated by observations made during a former period of association with the European Laboratory, Commonwealth Institute of Biological Control (Franz, 1954), a new study has been conducted since 1954. Attempts were made to contribute to the understanding of the population dynamics, particularly the causes of declines in outbreaks of the balsam woolly aphid. The techniques used and part of the results are reported here.

The principle of the study was to observe quantitatively the populations of aphids in three comparable and small plots on the bark of each of 13 trees. The first plot was open, being marked only on the bark; the second was protected from predators by a wire-mesh shelter treated with contact insecticide; the third had a similar, untreated wire-mesh shelter but predators were allowed access through two small holes in the sides, thus avoiding the influence of different microclimatic conditions, as used in the mechanical check method by DeBach and co-workers (1949). *A. piceae* is particularly well suited to this type of experimental study since this species lives its entire life, and is always observable, on a nearly flat surface of bark.

The aphid population in the plots was counted at short intervals using a plotting apparatus designed recently (Karafiat, 1955, 1957). In employing this apparatus the position of each individual aphid is plotted on a sheet of paper using an enlarged scale by means of a pantograph, as shown in Fig. 1. The instar and cause of mortality, if any, of each aphid is recorded. All plots were photographed at regular intervals. The combination of plotting and analyses of serial photographs provided detailed information on the fate of many thousands of aphids, thereby establishing what might be referred





Fig. 1. Plotting apparatus (pantograph) used for population counts in the field.

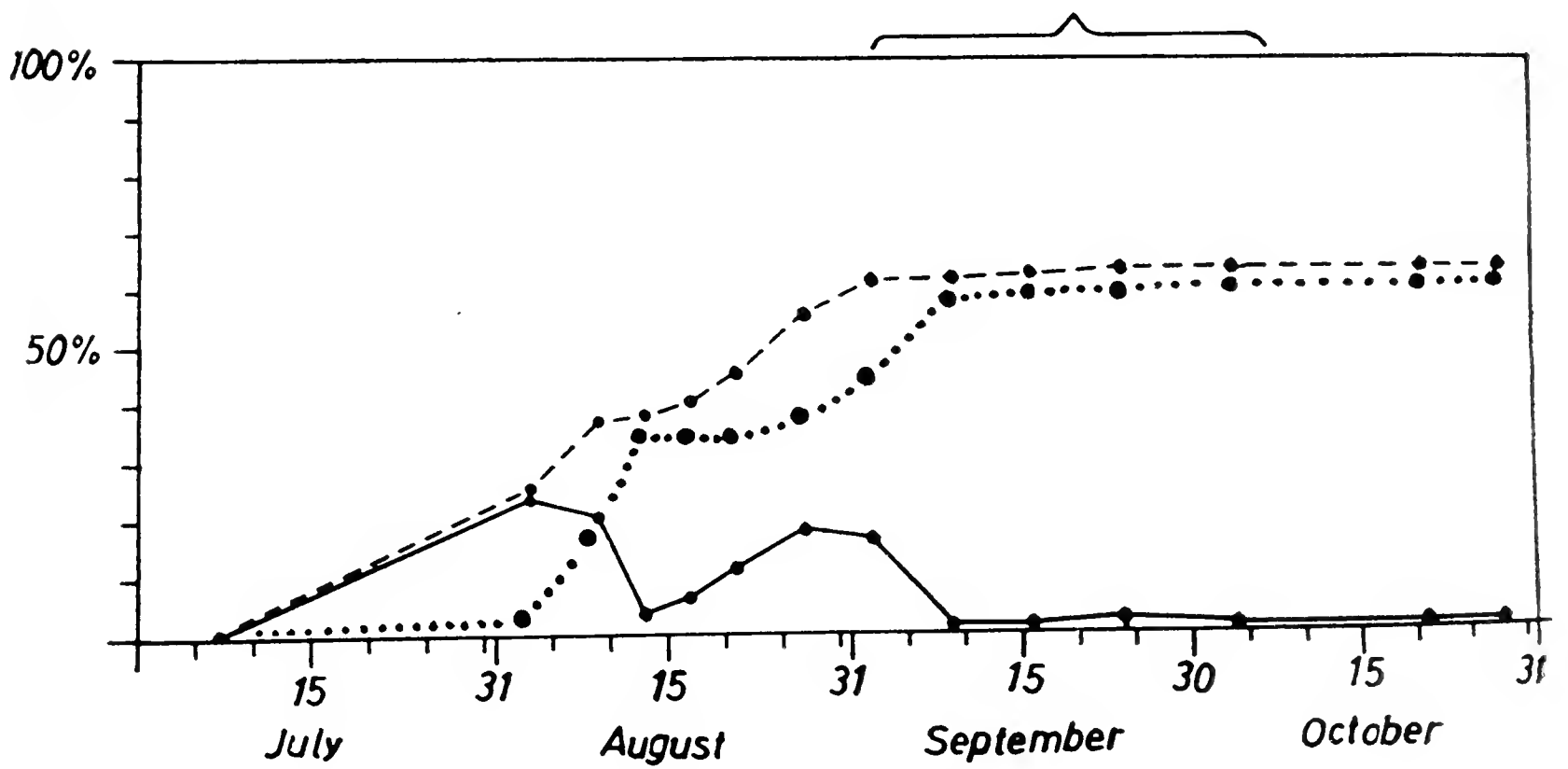
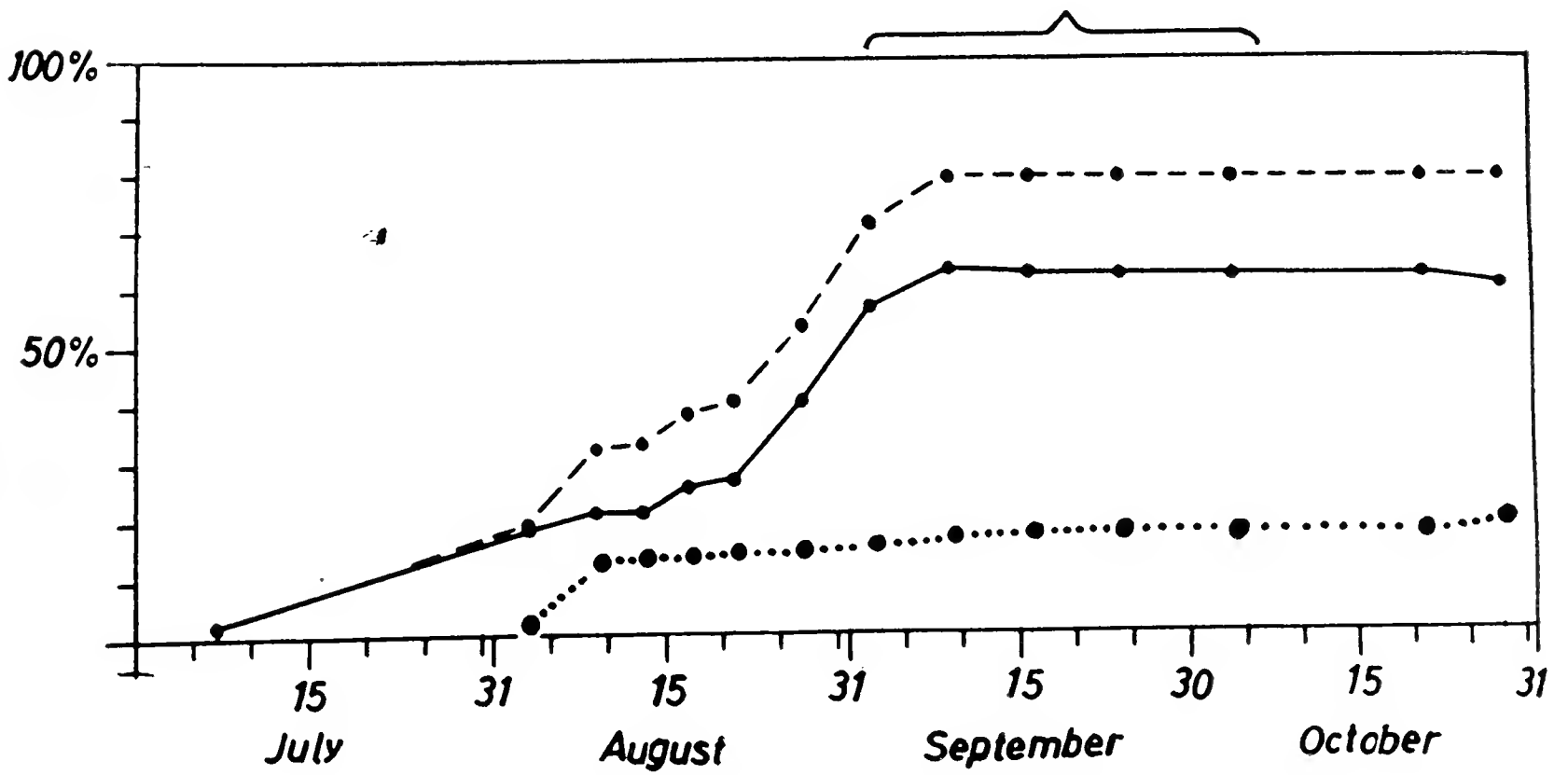
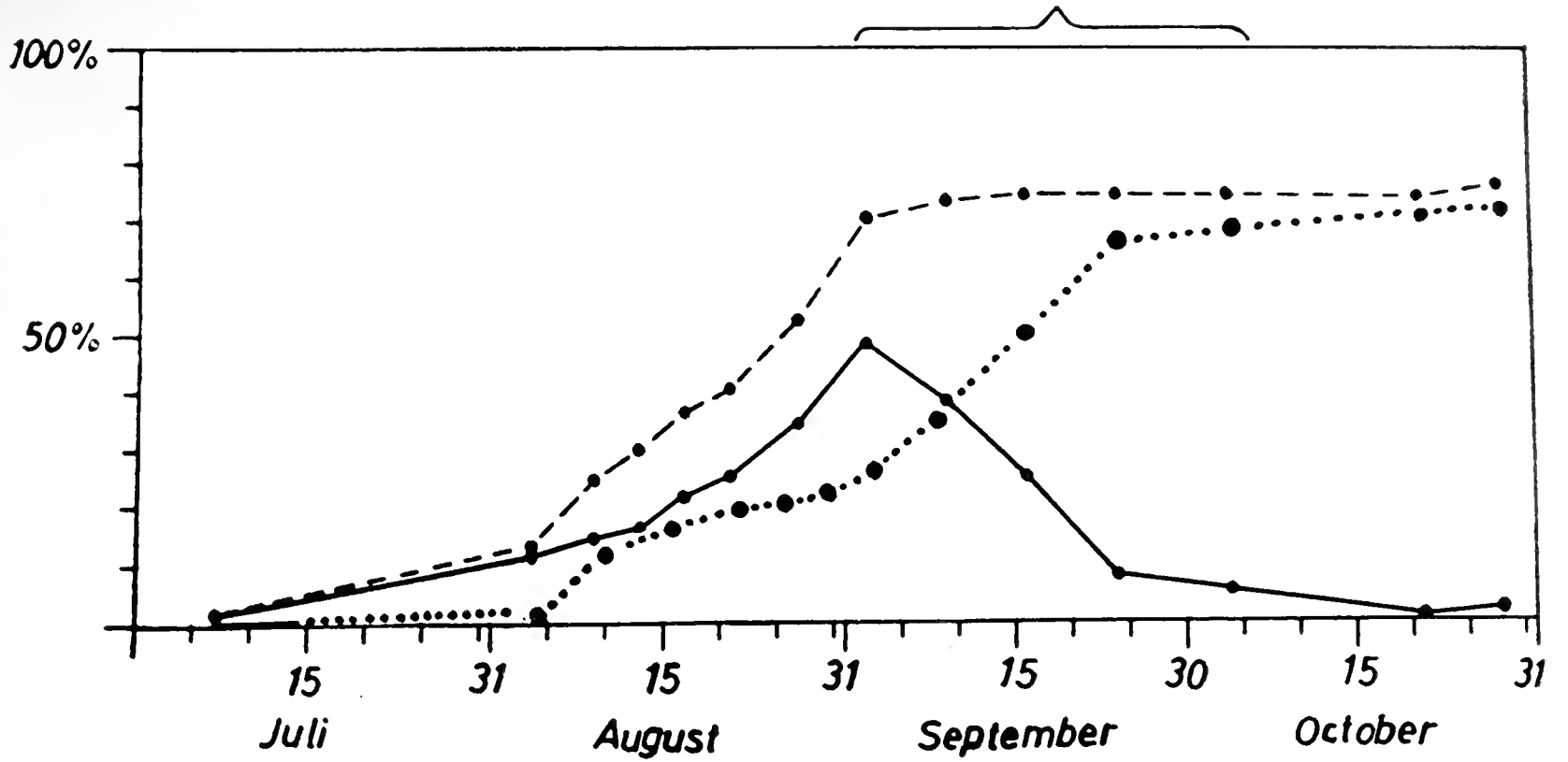
to as life tables of this species. The help of Dr. H. Karafiat in the field work is gratefully acknowledged.

### RESULTS

As with most insects that are studied closely, the population fluctuation of *A. piceae* is influenced by a complex of biotic and abiotic factors. Two of these, the activity of predators and the reaction of the host plant proved to be of special importance. Their influence will be shown, first singly and then together. The results will be given in greater detail in a subsequent publication (Karafiat and Franz, 1956).

The effects of predators can be demonstrated by reference to a typical example of an infestation on a fir tree in our field station in the Odenwald. On the stem of an 80-year-old tree three plots were established in June 1954. The development and survival of the first instar larvae (neosistentes) that had settled shortly before and

Fig. 2. Increase (—•) and loss (····•) of a population of *A. piceae* in open plot (above), protected plot (centre), and partially protected plot (below). —•— = number of actually present living aphids. Brackets indicate period of main predator activity. First summer generation, total of 2<sup>nd</sup>, 3<sup>rd</sup> instar larvae and adults. Odenwald, Germany, 1954.





had remained dormant for some time was nearly alike on all three plots. The number of neosistentes decreased in all plots from July to September. Some died; the majority, however, developed further, to second and third instars and to adults with parthenogenetic reproduction. The close similarity between the development of these populations in the open and in the protected areas reveals that first instar larvae are not usually attacked by predatory insects. The neosistentes are apparently an unsuitable prey.

Further development of the population of immature and adult aphids on the three plots proceeded in a different way. From a rather similar starting density, the populations of growing or adult aphids actually present were altered by: the continuous addition of new sistentes that terminated their dormancy, and the loss of others by death. Curves for the three plots are shown in Fig. 2.

In the *open* plot this interaction proceeded as follows: Until the end of August the total additions outnumbered the losses and therefore, the number of living aphids actually present increased. After the end of August fewer aphids reached advanced instars, but more of them died. The time when the curve dropped coincided with an accumulation of predators. This, as well as the marks of feeding on dead aphids suggests that population losses might be caused by predators.

The effects of predation were proved conclusively by comparison with populations *protected from predators*. On the protected plot, there was no sudden decrease in numbers of aphids in September. The curve for growing and adult individuals remained constantly high. The low mortality observed was caused by a dipterous larva which for a short time entered in spite of all vigilance.

The interaction between population increase and mortality was most clearly demonstrated on the plot protected with wire mesh but with small entrances for predators. The number of living aphids actually present increased and decreased in turn. This might be explained by the fact that predators prefer sheltered places. In the plots covered with wire mesh the predators remain until the stock of edible aphids is depleted, after which they leave. Before predators reenter the cage, the number of growing aphids can build up again.

On all the other caged and open plots, with the same favourable bark conditions, the population fluctuations were principally the same. In spring, the effect of predation was more drastic than in autumn. Continuation of the infestation during reproduction depended upon the number of neosistentes that were able to hatch before the succession of predators eliminated the adults and their eggs. In autumn, the importance of predators proved to be more closely related to weather conditions than in spring. By using the method described, the marked influence of predation could be measured and the time of action of the predators defined.

As mentioned previously, the change of the bark as affected by the sucking of the aphids is another important limiting factor. Studies by Balch (1952) and Kloft (1955) already point in this direction. Kloft (1955) indicates that as a consequence of a continuous mass outbreak all parenchymatic tissues in the peripheral bark die, down to a depth of 3-4 mm. In view of the usually sudden decline of populations after a few years Kloft believes that the degeneration of the bark is the decisive causative factor.

To judge and compare both factors, the activity of predators and the exhaustion of the bark, field experiments were set up that separated their usual interaction. The following results were obtained: In our predator-free plots the population of aphids continued after disappearance of the general infestation on the open stem. Protected populations often persisted one to two years after the decline of the surrounding unprotected population. It is characteristic that the population density of such protected plots decreased slowly (Fig. 3). The reason for this is the gradually reduced suitability of the bark as feeding site for the aphids. There originated a secondary cork cambium at a depth of 1.3 mm. The external layers of the cork cambium died and no longer offered any feeding possibility for the aphids. Finally, the bark was so badly damaged that neosistentes could only settle on very limited areas. The adults were more or less sterile. One might argue that in these experiments  $3.5 \times 5$  cm. plots are too small to make conclusive deductions for the population of aphids on the whole stem. If, however,

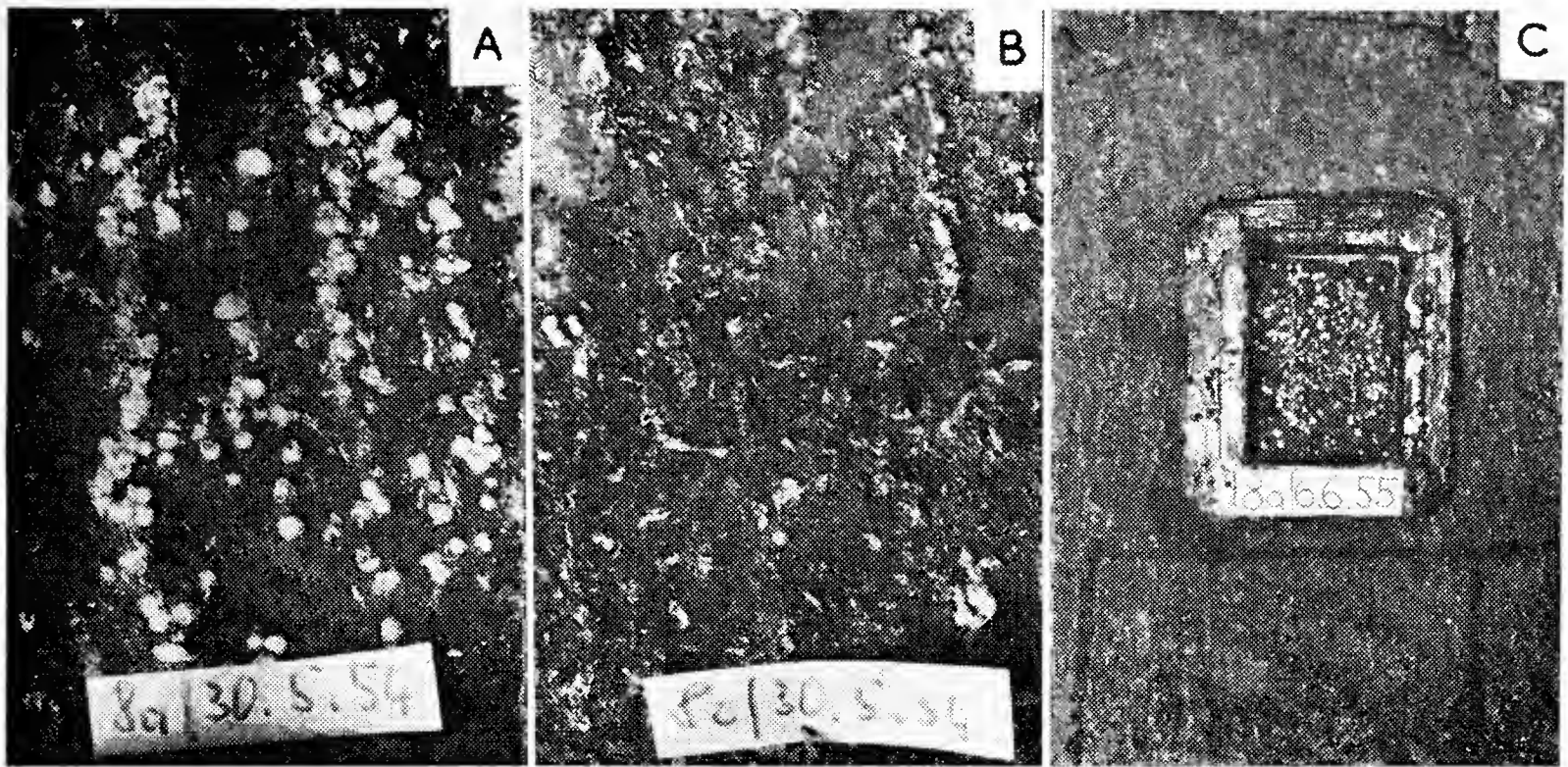


Fig. 3. Continuation of the outbreak of *A. piceae* in predator-free plot: (A) Plot 8a on May 30, 1954, full of living aphids producing wax wool. — (B) Neighbouring open plot 8c shows effect of predation on the same day. — (C) Predator-free plot 8a and surrounding bark one year after disappearance of the outbreak on the open stem. Note reduction of large wax wool spots indicating living mature aphids.

the extensive infestation joining the plot had a distant effect operating through the bark, it could also have had ample opportunity to damage the predator-free plot in years before the decline of the population. Furthermore, the results of our bark anatomy studies indicate a restricted and very local effect of sucking aphids.

The proportional effect of both mortality factors on retrogradation is variable. The decline occurs always later on predator-free plots than on open ones. Examples were observed of the dominating effect of bark degeneration, of predator activity, and of more or less equally important effects on both factors in unprotected populations. The curve of first instar larvae in predator free plots settling from generation to generation served as criterion of bark quality (Fig. 4). Healthy bark allows a characteristic, steep numerical increase of settled crawlers after each period of reproduction (Fig. 4 A). Degenerated bark shows up as a flat curve for new, settling first-instar larvae in spite of numerous crawlers present (Fig. 4 B). The importance of other mortality factors will be referred to rather briefly. Rain was detrimental when in the form of a down pour by washing away some aphids, and soaking rain by building up a thin layer of water on the surface of the stem which, through adhesive forces, prevented the wandering of the crawlers. As occurred last winter (1955/56), extreme frost might kill all hibernating second and third instar larvae. Some local populations have been almost eradicated by frost. In our study area, the infestation continued for a while on such trees that, for reasons not yet fully understood, harboured mostly first instar larvae during hibernation. The outbreak was finally terminated by the concentrated attack of predators (mainly *Pullus impexus* Muls. and *Laricobius erichsonii* Rosenh.) which showed a higher cold-hardiness than the overwintering advanced instars of the aphid. First-instar larvae tolerate, as shown by Balch (1952), winter temperatures of  $-35^{\circ}\text{C}.$ , which is also the limit tolerated by their host tree. Thus, sometimes abiotic factors also very effectively reduce the population.

As far as is known, however, in average years the effect of predators and bark degeneration are the key factors determining retrogradation. The following simplified scheme shows how both these factors might interact (Fig. 5). After the apparent start of an outbreak the population density of the balsam woolly aphid increases for some time, although predator activity increases and the suitability of the bark as food decreases gradually. As shown previously, both factors can be separated experimentally since, in principle, they do not depend on each other. Actually, however, both interact because through the decreasing suitability of the bark as feeding site for the aphids the area susceptible to infestation is continually reduced; thereby, the effectiveness of

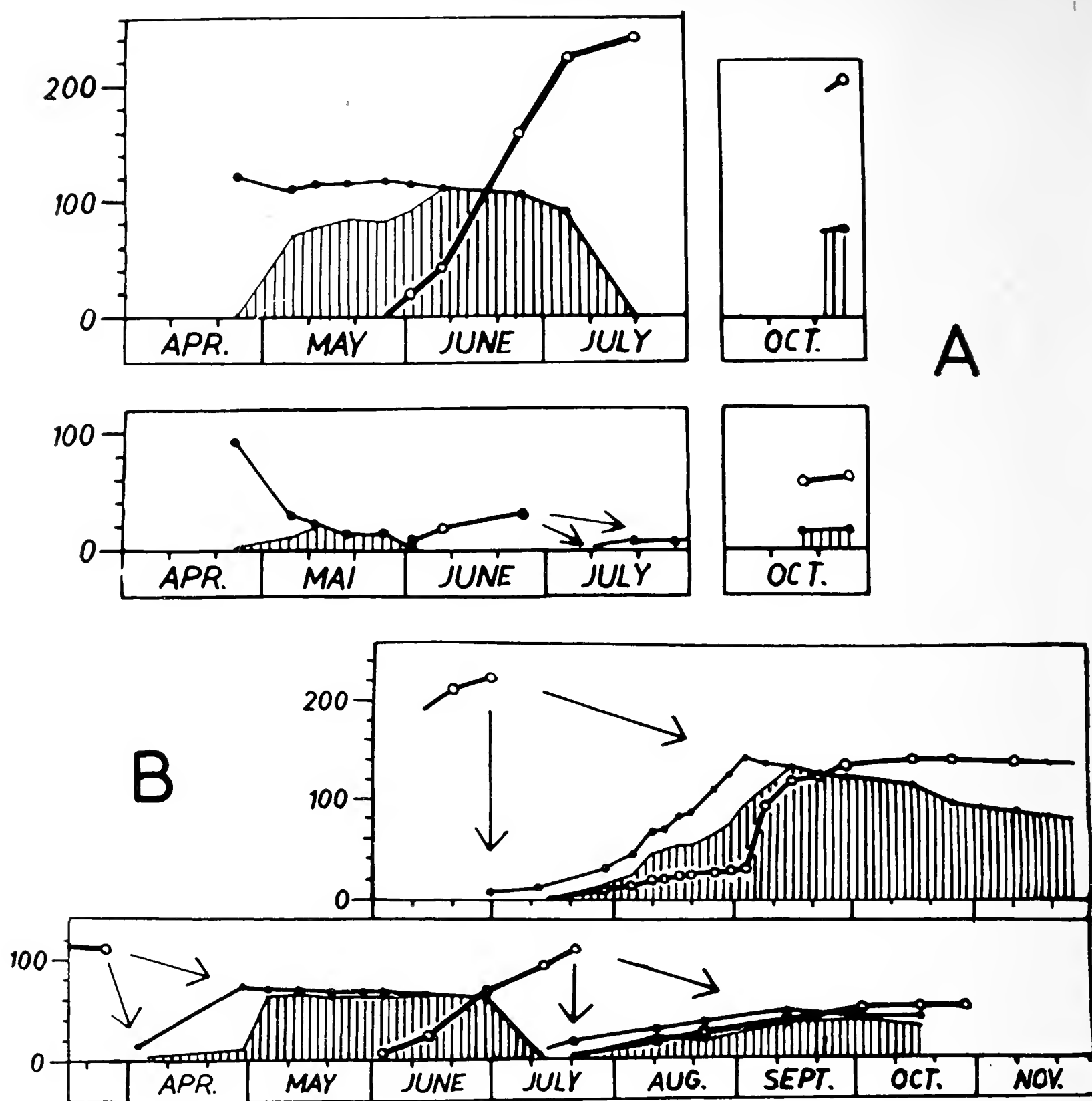


Fig. 4. Steep numerical increase of settling first instar larvae (—○—) of *A. piceae* in protected area on healthy bark (A, upper part) as compared to flat curve on degenerated bark (B). —●— = total number of living 2nd, 3rd instar larvae and adults. Striped area: number of egg laying adults. — Fig. 4A, lower part: Population decline in open plot beside protected plot shown in upper part. Decline primarily caused by predators.

predators is enhanced, regardless of their absolute population increase. When these factors, together with weather and overcrowding, destroy more aphids than can be added by egg production, then the characteristic collapse occurs on the stem, as shown by the sharp decline of the curve. The time delay of  $1\frac{1}{2}$  years shown between the curve of aphid density and food suitability corresponds with the average prolongation of the infestation on predator-free plots. Both curves have to be considered as laterally moveable to take into account the variation of actual observations.

Finally, an essential difference in the effect of mortality factors might be mentioned. Both together contribute, as has been shown, by limiting the time of the gradation. The predator complex is, in addition, capable of limiting the extension of an outbreak in space. The observation of many infestations shows that, in Europe, outbreaks usually do not comprise more than one to a few dozen stems. Infestations, therefore, do not expand rapidly in spite of the known capability of the aphid to spread. This is caused primarily by predators that have to search the marginal zones of the infestation most thoroughly during the decline of the outbreak in order to survive. Predators, therefore, are able to influence the development of the gradation

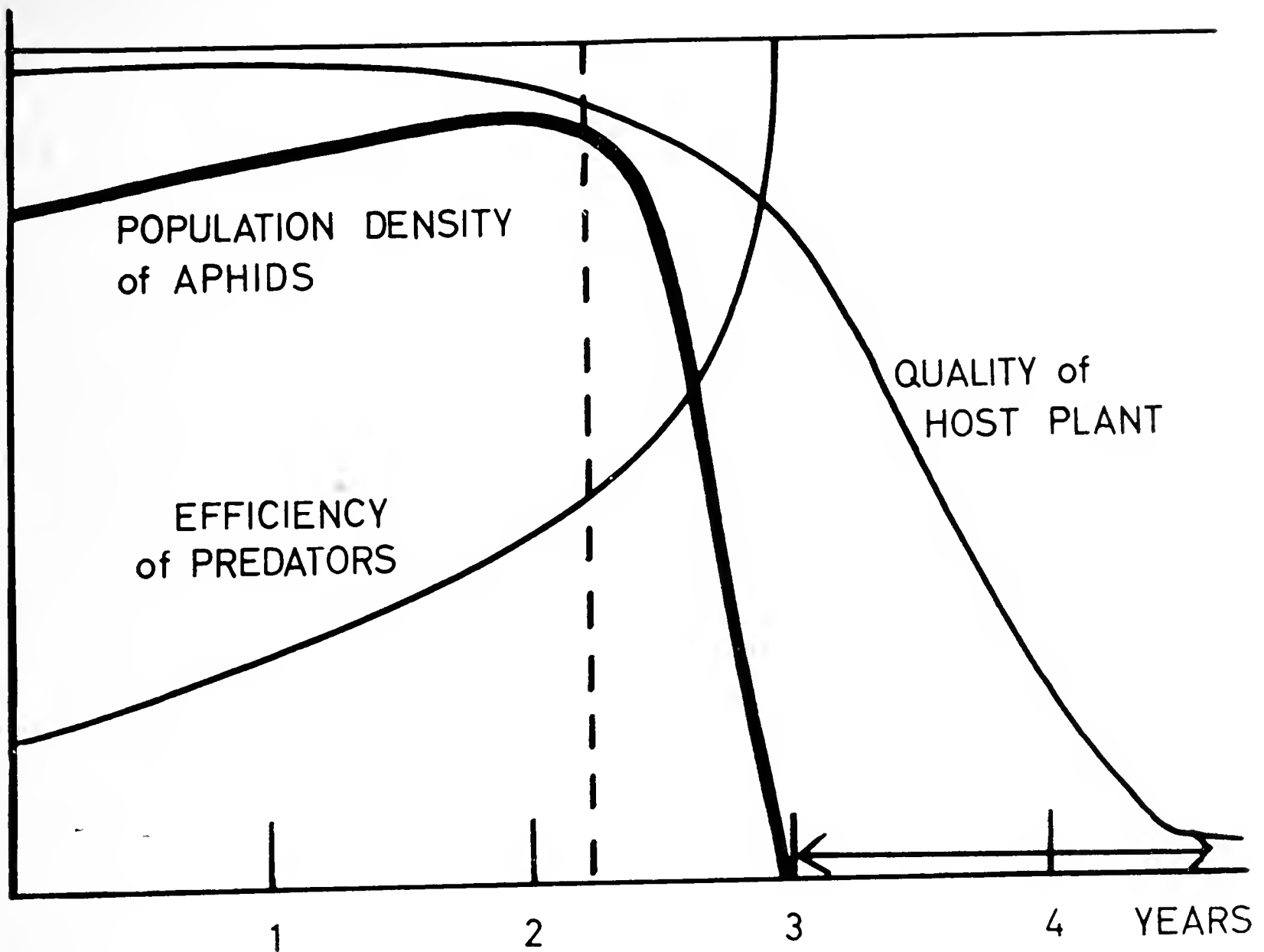


Fig. 5. Simplified scheme of interaction of predators and host plant as factors influencing population density of *A. piceae*. Arrow indicates average time-lag in the decline of outbreaks in predator-free plots as compared to open plots.

in time as well as in space, whereas the reaction of the bark has its effect limited to each individual stem. New gradations occur after regeneration of the bark, originating from the aphids that invariably remain in hidden places.

Still not enough is known about the whole complex of factors influencing the population dynamics of the balsam woolly aphid. The present paper throws some light on a part of the problem and demonstrates the suitability of this insect for the study of the interaction of predators with other mortality factors in the field.

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# *Adelges nüsslini* (Börner) (Homoptera: Phylloxeridae) and its Predators in Eastern France<sup>1</sup>

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## ABSTRACT

The life-history of *Adelges nüsslini* (Börner) (Homoptera: Phylloxeridae) in the Vosges Mountains of Eastern France is described and compared with that recorded for other parts of Europe. The insect infests the twigs of small firs and, less frequently, the trunks of old fir trees. The effects of infestations are described. A list is given of nine species of insect predators of *A. nüsslini*, with notes on their life-histories. Observations on habitat selection by the different predaceous species, and its significance in evaluating the role of each species as a biological agent of control, is discussed.

## INTRODUCTION

During 1950 and 1951 the writer collaborated with officers of the Commonwealth Institute of Biological Control in studies of *Adelges piceae* (Ratz.) and *A. nüsslini* (Börner) in Europe. The studies primarily involved the biological control of these adelgids, and included selection of the more abundant control agents for release in Canada against *A. piceae*. Investigations on *A. nüsslini* conducted by the writer are outlined in the present paper.

## NOMENCLATURE

Some confusion in the European literature has resulted from similarities between *A. nüsslini* and *A. piceae*. However, as shown by Marchal (1913), the two are biologically and morphologically distinct. The history of the nomenclature was reviewed by Balch (1952). Though both species are included in the genus *Dreyfusia* by some European investigators, the use of the genus *Adelges*, as proposed by Annand (1928), is followed in the present paper.

## DISTRIBUTION

*A. nüsslini* occurs throughout Central Europe as well as in the Scandinavian countries and the British Isles. Many European workers believe that the insect spread across the Continent from Asia Minor and the Caucasus region of the U.S.S.R. during the last half of the nineteenth century. It does not occur in Eastern North America, but has been recorded from California (Annand, 1928) and from Vancouver, British Columbia (Balch, 1952).

## DESCRIPTION OF STUDY AREAS

*A. nüsslini* was studied in the Vosges Mountains near Ribeauvillé, France. In this area there are extensive stands of fir, *Abies alba* Mill., lightly mixed with spruce (*Picea excelsa* Link.), pine (*Pinus sylvestris* L.), larch (*Larix decidua* Mill.), and several deciduous tree species. Infestations were limited to fir at altitudes up to at least 3,000 feet.

## TYPES OF INFESTATION

There were two distinct types of infestations: the more common involved the twigs and small branches of trees approximately 15 feet or less in height; and the other was limited to all or part of the main stem of large firs. Very occasionally there were heavy trunk infestations on trees with severe twig attack, but usually the outbreak was limited to one of the two habitats. Trees both in exposed areas and in dense shade were liable to either type of infestation.

## LIFE-HISTORY

*A. nüsslini* usually has a pentamorphic life cycle with migration by winged individuals between two host species. The primary host, on which a sexual generation

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develops, is the oriental spruce, *Picea orientalis* Carr., and the secondary host, on which the females reproduce parthenogenetically, is species of fir. In the Vosges, where there is no oriental spruce, the insect is limited to its secondary host.

Both first and second instar sistens larvae were present on the bark of infested trees during the winter months. Some of the neosistens molted to the second instar late in the autumn or during the winter, whereas others did not do so until April. Third instar larvae were present before March 15 and comprised 60 to 70 per cent of the adelgid population by April 5. Adults were first observed on March 23, and oviposition commenced about April 1. Most of the adults were dead before June 1, though a small proportion lived until about June 15.

The time and rate of development of the overwintering generation of *A. nüsslini* varied greatly. For example, all larval instars and ovipositing adults occurred simultaneously on many trees in mid-April. This uneven development was caused mainly by adelgids on the young twigs developing and laying eggs earlier than specimens on the main stems. In addition, development was slower on trees growing in dense shade. It is probable that this slower development rate in shaded areas resulted from lower bark temperatures, as noted by Börner (1927).

The fecundity of *A. nüsslini* varied greatly; adults on the young twigs of small trees generally deposited more eggs than those on the trunks of older trees.

The neoprogressiens larvae, which hatched early in May from the first eggs laid by adults of the overwintering generation on the twigs, moved to the needles of the new growth, inserted their styli, and immediately began to develop. There were four molts. Some of the adults produced were wingless progredientes each of which laid 10-15 eggs early in June. All of the larvae from these eggs were of the sistens type and settled on the bark and never on the needles. The remainder of the adults were winged sexuparae and were present in large numbers on the needles and new growth of fir during the first two weeks of June. A few sexuparae, which were subsequently noted on the needles of young *P. excelsa* growing near infested fir trees, did not oviposit. As noted previously, there is no oriental spruce, *P. orientalis*, in the Vosges. It, therefore, seems likely, as claimed by Marchal (1913), Chrystal (1926) and Hofmann (1937), that there is a sexual generation on oriental spruce only.

Sexuparae and progredientes were produced on all small trees with twig infestations. None was observed, however, on the needles or bark of large trees with trunk attacks.

All the larvae that hatched from eggs laid on the trunk by the overwintering generation, and the majority that hatched on the twigs, were of the sistens type. They settled on the bark of the twigs or trunk, and never on the needles. Most of these remained in the first instar until the following winter or spring; a few, however, particularly on infested trunks, molted three times and produced sistens adults in August and September. These adults laid less than 15 eggs each. These eggs produced sistens larvae that inserted their styli in the bark and did not resume development until the following winter or spring.

The life-history of *A. nüsslini* as outlined above, agrees in most respects with that recorded by European workers. However, Marchal (1913) claimed that only the neosistens stage overwintered in the neighbourhood of Paris. In the Vosges both first and second instars were present during the winter months. Hofmann (1938), working in southern Germany, also noted the occurrence of both instars during the winter. Schneider-Orelli (1950) noted a few third instar larvae in November in Switzerland, but none was observed in the present investigation. Chrystal (1926) claimed that, in England, a few adults oviposited in late June and early July. No sistens adults were observed at these times in the Vosges.

## DAMAGE

Considerable damage and mortality resulted from twig infestations on trees less than 15 feet in height. In heavy infestations the needles curled around the twigs and eventually turned yellow and died. Often the twigs at the top of the tree were killed first, but in cases of severe attack that involved both the trunk and twigs the tree died more uniformly. There was no abnormal swelling of the buds and twigs similar to

that produced by this insect on *Abies grandis* Lindl. (Chrystal, 1926) and by *A. piceae* on several species of fir (Balch, 1952).

There was no mortality nor apparent damage to large trees with trunk infestations.

### INSECT PREDATORS

Several predators of this adelgid have already been recorded: Hofmann (1938), working in Bavaria, listed the coccinellids *Aphidecta oblitterata* (L.) and *Exochomus quadripustulatus* (L.) and Syrphidae of the genera *Syrphus* and *Pipiza*; and Schneider-Orelli (1939) observed predation by *A. oblitterata* in Switzerland.

In the present investigation nine predator species, consisting of four coccinellids: *Aphidecta oblitterata* (L.), *Pullus impexus* (Muls.), *Anatis ocellata* (L.), and *Exochomus quadripustulatus* (L.); one derodontid: *Laricobius erichsoni* Rosenh.; one chrysopid: *Chrysopa ventralis* Curt.; two chamaemyiids: *Leucopis griseola* (Fall.) and *Neoleucopis obscura* (Hal.); and a syrphid: *Syrphus arcuatus* (Fall.); were observed.

The following notes summarize observations on the life-histories of these predators.

*A. oblitterata* (L.) occurred commonly on infested twigs and occasionally on trunk outbreaks. Both adults and larvae were predaceous on the second and third instar larvae, adults, and eggs of *A. nüsslini*; fourth-instar larvae also attacked the crawlers and progredientes. The coccinellid adults appeared on infested trees early in April, when adelgid oviposition was commencing. The predator eggs were laid in groups of 10 or less on the needles of the infested twigs, and, less commonly, on the bark. The egg stage lasted about seven days in nature. There were four larval instars; mature larvae pupated on the bark or needles after early June, and adult emergence commenced about a week later. Freshly-emerged adults mated and soon dispersed, and did not reappear on adelgid-infested firs until the following spring. Parasitism of the coccinellid larvae by an unidentified mermithid, and of the pupae by a phorid, *Phalacrotophora berolinensis* Schmitz, was observed.

*Pullus impexus* (Muls.) was almost entirely limited to trunk infestations. Its annual cycle was the same as that recorded in detail by Delucchi (1954). Briefly, eggs laid on the bark in August and September overwintered, and larvae hatched about the time the first adelgid adults appeared in April. There were four larval instars; pupation on the bark commenced about mid-May, and the first adults emerged about 10 days later, but did not oviposit until August. Both adults and larvae were predaceous on the second and third instar larvae, adults, and eggs of *A. nüsslini*.

*Laricobius erichsoni* Rosenh. was almost entirely limited to trunk infestations. The annual cycle of this derodontid agreed with that recorded by Franz (1953) in Germany; in general, adults emerged from the soil in early April and oviposited on the infested stems. Larval development was followed by pupation in the soil at the base of the infested trunks in June. Both adults and larvae attacked the second and third instar larvae, adults, and eggs of *A. nüsslini*.

Larvae of *Leucopis griseola* (Fall.) ate the second and third instar larvae, adults, and eggs of the spring generation of *A. nüsslini*, and pupated in the soil after mid-May. Adults that emerged in August apparently overwintered, and egg-laying commenced early in April. Feeding by this species was mostly restricted to adelgids on twigs. Larvae of another chamaemyiid, *Neoleucopis obscura* (Hal.) were active on infested trunks but rarely on twigs. There were two generations annually; adults emerged early in June and again in August. First and second instar larvae overwintered.

Larvae of *Chrysopa ventralis* Curt. ate second and third instar larvae, adults, and eggs of the spring generation on both twigs and trunk, and formed cocoons late in May and early in June. Adults emerged and oviposited early in July. The larvae that hatched from these eggs hibernated in the second larval instar on the infested trees.

Predation by *Anatis ocellata* (L.) and *E. quadripustulatus* (L.) was observed only occasionally. Adults and larvae of both species fed on the spring generation of *A. nüsslini*; adults emerged in June and July, but did not attack the adelgid again until the following spring.

Larvae of *Syrphus arcuatus* (Fall.) were recorded occasionally on infested twigs. No detailed observations were made on its life cycle.

## GENERAL DISCUSSION

*P. impexus*, *L. erichsoni*, and *N. obscura* have been introduced and established in infestations of *A. piceae* in Canada. In Europe none of these predators has previously been recorded as attacking *A. nüsslini*, which usually infests twigs and small branches; in the present study, however, all were collected on stem outbreaks, though they were usually absent from adjacent twig infestations. The only specimens taken from infested twigs were on firs with both stem and twig attack.

Though adelgid development in spring was slightly more advanced on the twigs than on the trunk, suitable host stages for development of all the predator species were present simultaneously in both habitats. In addition, experimental studies showed that predator larvae matured and pupated if fed adelgids from either environment. It is likely, therefore, that characteristics of the prey environment, and not of the prey itself, explain the almost complete restriction of the three predators to infested stems. Further evidence of their preference for this habitat is shown by the occurrence of all three as predators of *A. piceae*, a predominantly stem-infesting species (Delucchi, 1954).

The habitat selection of *A. obliterated* and *L. griseola*, was not so distinct. *A. obliterated* was observed in twig outbreaks of *A. nüsslini* (Hofmann, 1938; Schneider-Orelli, 1939) and on stems infested by *A. piceae* (Delucchi, 1954); whereas *L. griseola*, though predaceous on other aphids (Schutze, 1936; Pruthi and Bhatia, 1938) and on *A. piceae* (Delucchi, 1954), has never been recorded on *A. nüsslini*. In the present study, though active in both habitats frequented by *A. nüsslini*, both predators were much more common and abundant on twigs than on trunks. It is again probable that characteristics of the habitat, and not of the prey itself, influenced the distribution of the two species.

The characteristics of each environment that determine its attractiveness to the different predator species were not investigated; however, it is possible that bark roughness and exposure to direct sunlight are involved.

Selection of specific habitats by parasitic insects prior to the location of suitable hosts within these environments has been observed by many authors. A host occupying two different habitats may, therefore, largely escape parasitism in one of these; Walker (1939) showed that larvae of *Cephus pygmaeus* (L.) (Hymenoptera: Cephidae) infesting barley were parasitized to a lesser extent by the ichneumonid *Collyria calcitrator* (Grav.) than those infesting wheat. In the case of several coccinellids Thompson (1951) noted a high degree of specificity in environment selection. Further evidence of this phenomenon is given in the present study, where predators of several families fed commonly on *A. nüsslini* in one environment but rarely in another, often adjacent, one. The significance of this should be considered in attempting to estimate the future effect of introduced predators of *A. piceae* in Canada, where this adelgid is common on infested stems and also causes considerable damage on the small branches and twigs.

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# Preliminary Investigations on the *Adelges* Populations (Hemiptera: Adelgidae) Living on the Trunk of the Silver Fir

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## ABSTRACT<sup>1</sup>

First, the taxonomic status of the European silver fir woolly aphids is reviewed and it is recommended to subdivide the two species, *Adelges piceae* Ratz. and *A. nüsslini* C. B., into four ecologically and partly also morphologically distinguishable forms, one of which is to be raised to the level of a new species.

The damage caused by the different adelgids on the different kinds of firs is discussed in relation to the imported Canadian form, living on *Abies balsamea* (L.) Mill.

The second part deals with the ecology and population dynamics of *A. piceae* and *A. nüsslini*, forma *schneideri*, both forms living exclusively on fir trunks in Europe. The abundance and distribution of the endemic density of these aphids and its relation to environmental factors, especially to forest composition, etc., is outlined in a special chapter.

The hypothesis on the release of an endemic density to an epidemic one, as developed in collaboration with W. Kloft, is examined and data are given on the progress of a mass outbreak and on its occurrence in different forest types.

The factors regulating the population density and terminating a mass infestation are worked out on the basis of field observations and experiments in cages. Among the complex of control factors, special attention is given to the predators in connection with their importation for biological control into Canada.

<sup>1</sup>The paper will be published in full details and with supplementary informations, under the abovenamed title and in English language, in the German journal "Zeitschrift für Angewandte Entomologie", 42, 1958, edited by Prof. Dr. W. Zwölfer Institut für angewandte Zoologie, München (Munich), Germany, published by Paul Parey, Berlin and Hamburg.



Notes on the Predators of *Adelges piceae* Ratz.  
and *A. nüsslini* C.B. (Hemiptera; Adelgidae)  
in Sweden

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ABSTRACT

Within the long-term program of biological control of *Adelges piceae* in Canada, collection of predators of this pest was recently extended to Sweden, and a report on the predator fauna in that country is given in comparison to our middle European predator complex. While some important predators, as *Laricobius erichsoni* and *Pullus impexus*, are absent in the Swedish fir afforestations, and others, like *Cremifania nigrocellulata* and *Aphidoletes thompsoni*, are comparatively rare, two predators, namely *Aphidecta oblitterata* and a not yet identified *Syrphus* species, both associated mainly with *A. nüsslini*, occur in higher abundance in Sweden than in middle Europe, and offer greater chances for collections there.

On the island of Visingsö and at Mount Omberg in Southern Sweden, we studied intensive infestations of *Adelges* in the spring of 1956. In these localities, there were plantations of silver fir, *Abies alba* Mill., some dating back to 1860, and of balsam fir, *Abies balsamea* (L.) Mill. The balsam firs were generally not attacked by aphids, but the silver firs were heavily infested either by the twig aphids of the typical *A. nüsslini* form or by the trunk aphids of *A. piceae*, forma *typica*, and by the *schneideri* form of *A. nüsslini*. (Pschorn-Walcher & Zwölfer, 1956a).

Two things were striking: the unusually great number of trunks infested by *A. nüsslini*, f. *schneideri*, and the high endemic density of the *A. piceae* populations.

With respect to the *schneideri* form of *A. nüsslini*, we have seen fir stands in which, on an average, every third tree must have been heavily infested in 1955, while in the spring of 1956, when we visited the area, about two-thirds of the old infestation have disappeared, apparently through the combined effect of overcrowding, lack of food on certain trees, and of winter mortality, the latter having been much less important than in middle Europe.

As to *A. piceae*, on the other hand, we found only very few really heavily infested trees, while the great majority of the trunks were infested by an aphid population, the stage of which one might call intermediate between a normal, endemic density and a mass infestation. A census made in such a forest showed that approximately three-fourths of all available firs were infested by a 5- to 10-fold or even higher endemic density than in middle Europe. In Switzerland, where we have examined the population density in 27 different fir stands, we have always found a great number of trees infested by a low, endemic population, say 1-100 aphids per sq. yd. of bark surface, and a few firs, comprising never more than 25% which were in the phase of a mass propagation of the trunk aphids (Pschorn-Walcher & Zwölfer, 1956b). In Sweden, we counted only very few trees exhibiting either a normal density in our middle European sense or a mass infestation, but a great number of firs apparently carrying in 1955 as well as in 1956 a population of a considerably higher endemic density. Whether this high level of the normal stock of *A. piceae* and the more concentrated trunk infestations by *A. nüsslini*, f. *schneideri*, in Sweden are dependent upon an incomplete predator complex remains to be proved.

For a regional comparison, the predators can be classified into three groups: 1) species evidently absent in Sweden, 2) species less abundant in Sweden than in middle Europe, and 3) species of the same or of greater abundance in Sweden than in Switzerland.

Among the first group are the two important beetles, *Laricobius erichsoni* Rosenhauer and *Pullus impexus* Muls. Neither were they accidentally introduced into the Lake Vettern area nor have they, so far, reached this country naturally.

The second group, including species of minor importance, contains the dipterons, *Cremifania nigrocellulata* Czerny, *Aphidoletes thompsoni* Moehn, *Syrphus lapponicus* Zetterstedt, and probably the *Cnemodon* species and *Leucopis griseola* Fallen.

The record of *C. nigrocellulata* is new for the Swedish fauna. We found about 100 females at Visingsö, but only two in the more extensive infestations at Omberg, and because of its patchy distribution and the fact that it was not found by the Swedish entomologist Traegardh 25 years ago (1931) it is likely that *Cremifania* is a rather recent guest in Sweden.

*A. thompsoni*, also not yet mentioned from Sweden, was even more rare. We saw only two females at Visingsö and, in spite of our special attention to gall midges, we were not able to trace more of them.

*S. lapponicus* is recorded in the previous papers on *Adelges* by the name *Syrphus arcuatus* Fallen, both species being listed as identical in the palaearctic keys by Sack. Recent investigations in Britain (Coe, i.l.), however, have proved differences and our *Syrphus*, feeding on *A. piceae* in middle Europe is, in fact, *S. lapponicus* Zetterstedt, a form said to be present in North America. In the Swedish infestations, we found only one larva and an old puparium of this species.

We have not yet determined whether the adelgid feeders, *Cnemodon dreyfusiae* Delucchi and Pschorn-Walcher and *C. latitarsis* Egger, occur in Sweden or not. The single black hover fly, we observed on an infested tree, escaped capture, and our intention to examine material collected by other entomologists in Sweden is not yet fulfilled.

*L. griseola* is rare in middle Europe. In Sweden, we have not found it, in spite of being originally described from Scandinavia.

The third group of predators, of some higher abundance in Sweden, includes the lacewing, *Chrysopa prasina* Burm. (= *C. prasina ventralis* sensu Killington), the ladybird, *Aphidecta oblitterata* L., the chamaemyid fly, *Leucopomyia* (*Neoleucopis*) *obscura* Hal., and an unknown hover fly, probably *Syrphus punctulatus* Verall.

The lacewing is mainly associated with *A. piceae*, and is rare on twigs infested by the typical *A. nüsslini* and even less frequent on trunks covered by the *schneideri* form of *A. nüsslini*. As *C. prasina* exhibits a very polyphagous habit, its introduction into Canada has been omitted.

The coccinellid *A. oblitterata* prefers *A. nüsslini* populations on the branches and also its *schneideri* form on the trunks. Since both these forms are dominant in Sweden, *A. oblitterata* was more abundant here than in middle Europe. This species is important because of its special capacity to prey on twig aphids, and of its remarkable ability to trace out very slight and scattered host populations. In the jungle of young firs at Visingsö infested trees often are isolated and separated from one another by great distances, but, in spite of this patchy distribution, the *Aphidecta* beetles had succeeded in finding most of them.

*L. obscura* is by far the most abundant Swedish predator of both the trunk infesting aphid forms, while it doesn't seriously attack the twig aphids (Traegardh, 1931). This species, already established in Canada and the United States (Balch, 1952), has the disadvantage that its density is primarily dependent upon the host density. Heavily infested trees with a whitish look are evidently preferred for oviposition.

Finally, there was an unknown *Syrphus* species, found as a regular predator of the twig aphids, *A. nüsslini*, f. *typica*. It must be a very early species for we found its young larvae on our arrival at mid-May, and thus it must have been on the wing already in April. The larvae prey exclusively upon twig aphids, and we have never found them on the trunks of older firs. As they commence feeding with the start of oviposition of the hibernantes of *A. nüsslini*, they prey largely upon the first aphid eggs which give rise to the needle sucking progredientes. When the syrphid larvae become fullgrown, by the end of May or early June, the eggs of *Aphidecta* have just hatched, and the sequence of the twig predators is now continued by this species.



The syrphid larvae fasten themselves upon the twigs or needles and go into diapause. According to our experiments, this diapause seems to be of a very total nature. Dr. F. Schneider, a Swiss specialist for syrphid larvae, has examined the physiological stage of the imaginal disks of our material, and he believes that it may belong to an univoltine or to a bivoltine species. Thus it may be *S. punctulatus* Verall, an early, univoltine, wood-inhabiting form, specimens of which were captured in the Swedish infestation areas, as well as on firs in Switzerland.

Our Swedish observations did not uncover any "new" species of predators, not found in the middle European forests. However, at least two species, namely *Aphidecta oblitterata* and the unknown *Syrphus*, could be more readily collected in Sweden than in Switzerland. The other species, such as *Cremifania*, *Aphidoletes*, *Cnemodon*, etc., are rare in Sweden. As the climatic conditions in the Lake Vettern area are similar to or even milder than those in the higher parts of our Swiss investigation area, a collection of these scarce predators in Sweden does not seem very rich in prospects. But as our observations include only the course of one season, this should not be taken as a final recommendation.

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### DISCUSSION

J. FRANZ. You gave new names to two forms of *Adelges piceae*. Do you agree with the generally-accepted opinion that only such "forms" should be named that have differences of an innate or genetic nature? If so, what part of the differences of these forms mentioned in your paper are caused by external conditions, and what part by innate differences?

H. PSCHORN-WALCHER. The real taxonomic status of the different forms of *Adelges* in Europe is not yet fully elucidated. Work on this subject is in progress. That is, why we called our proposal a preliminary one and why we used the neutral term of a "form"; also mainly for practical reasons. I, personally, have some doubts whether the present taxonomic units are fully satisfactory to those type of insects like *Adelges* or other aphids with a similar complicated cycle.



# Climatic and Biocoenotic Aspects for the Collection of Predators of *Adelges piceae* Ratz. (Hemiptera: Adelgidae) in Europe

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## ABSTRACT

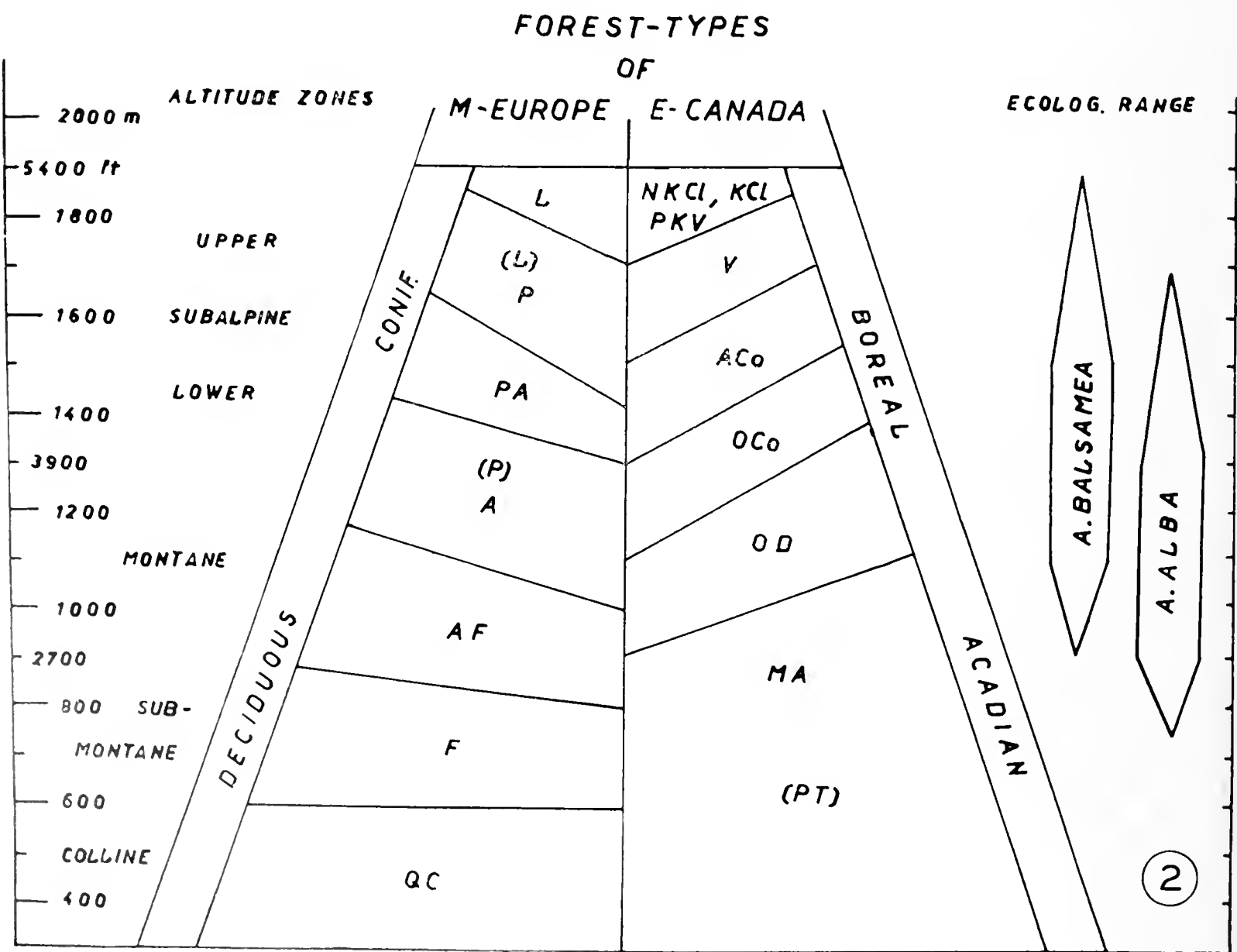
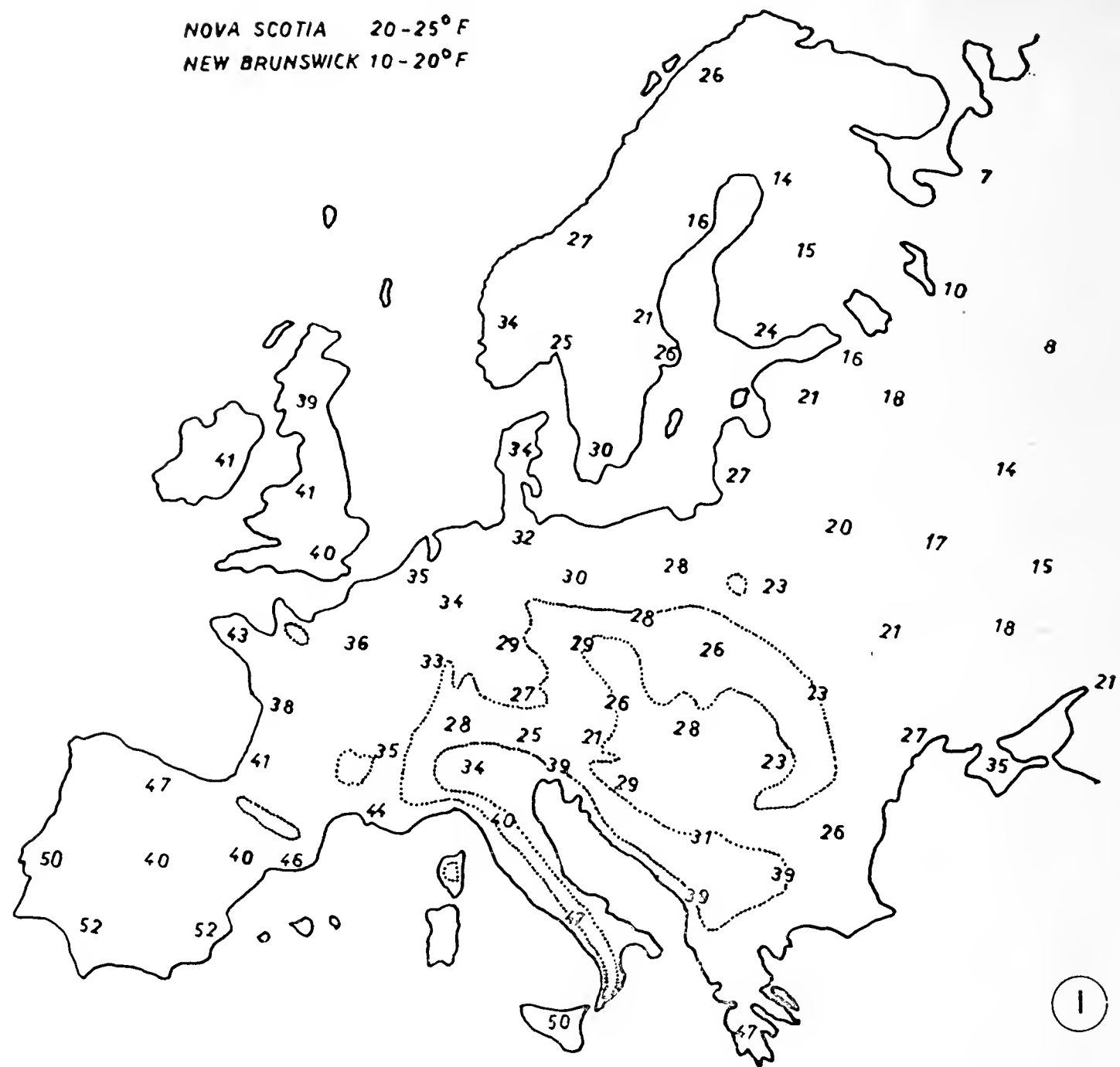
An attempt is made in this paper to outline the most suitable areas for the collection of predators of *Adelges piceae* Ratz. in Europe, by means of a climatic and biocoenotic comparison of the infestation districts in Canada and in Europe. It is the author's opinion that a more careful choice of the collection areas in Europe, — i.e. the collection of predators in plant associations most closely related to those of the overseas infestation areas — would enhance the chances for a successful establishment of the introduced beneficial insects. Furthermore, suggestions are made to prove this hypothesis by suitable field experiments with the imported material.

The purpose of this paper is to apply one of the first principles in biological control work to the special case of forest insects introduced from Europe into Eastern Canada, with particular reference to the balsam woolly aphid, *Adelges piceae* Ratz. According to this view, in importations of foreign predators, the collection area abroad and the place of the intended establishment of the introduced beneficial insects should agree as much as possible in their climatic and biocoenotic structure. This principle is based on the obvious supposition, that the acclimatization of a given species to the new environment will be more easily accomplished, if the material is imported from an area with similar ecological conditions.

The balsam woolly aphid has become established in the peripheral parts of the Eastern Provinces of Canada which are known as the Maritime Provinces. When we compare, however, the climatic conditions of Nova Scotia or New Brunswick with our European climate, we note that these countries exhibit temperature conditions, which would be called by us highly continental ones, though the relatively high precipitation modifies this statement somewhat. Above all, the very low winter temperatures seem to be one of the most important factors in the adaptability of European insects to the Canadian environment, and special care should, therefore, be taken to select parasite populations, which have originated in areas with severe winter conditions in Europe.

Winter temperatures like those at Fredericton, N.B., for example, are restricted to the middle and northern parts of Scandinavia and Russia, to the Baltic coast and eastern Poland, and to some countries within the Alpine and Carpathian Region (Fig. 1). On the other hand, the warmest winters are to be observed in England, France (except the eastern parts), Belgium, the Netherlands, in middle and northern Germany, in Denmark, and in southwestern Scandinavia, as well as in the Mediterranean region. These latter countries show the least similarity to the weather conditions in Eastern Canada.

Within the forenamed countries having a greater climatic correspondence to the areas of balsam infestation in Canada, we must distinguish between natural and artificial distribution areas of *Abies alba* (Fig. 1). Indigenous forests of silver fir are restricted to the mountainous parts of western-, middle-, southern-, and south-eastern Europe, while at lower elevations, and in northern and northeastern countries, as well as in the British Isles, only afforestations are to be found. It was an early supposition, and it has in fact been proved, that the predator complex of the now widely distributed *A. piceae* is much more rich in species in the natural and adjacent distribution areas of its host than in the remote or even isolated fir plantations, as for example in northern Germany, in England, or in Sweden (see the Congress paper by Pschorn-Walcher and Kraus). Consequently, in our example, and probably in most cases of biological control, investigations with the intention to find as many predators (or other useful organisms) as possible should preferably be undertaken within the original distribution area of the host, while the selection of specially adaptable strains of a



generally distributed predator species also the secondary areas of host distribution, which may sometimes show a greater similarity to the environmental conditions of the importation area, have to be considered. Thus, in our special case, the collection of the widely distributed *Aphidecta oblitterata* L. may offer greater chances from Sweden than from Switzerland, because of the greater correspondence between Northern Europe and Eastern Canada in general. For most of the other collections, of more specific predators, however, we are directed particularly to the middle European mountains, showing among the originally fir containing areas the best correspondence to Eastern Canada. Within that region, especially the eastern parts, as the eastern Alps in Austria, the Bohemian and Carpathian mountains as well as the more inneralpine parts of Switzerland and Austria point to a sufficient agreement with the Canadian climate.

To clear up the ecoclimatic and biocoenotic relationships between the Eastern Canadian balsam forests and the Middle-European silver fir woods more thoroughly, a comparison of the plant associations involved may be useful.

Among the few works done in this field in Eastern Canada, the classifications by Nichols, (1935) Halliday, (1937), and, above all, the outstanding work by the Finnish silviculturist Kujala (1945) on the forest vegetation types of Canada, contain the most valuable references for us.

According to Halliday's classification, the balsam woolly aphid has spread into the white pine-hemlock region, and, up to now to a lesser degree, also into the pure coniferous forest formation. Progress in the latter direction must certainly be expected in future, as the recent increase in Newfoundland shows (Balch, i.l.). As also the white-pine-hemlock forests have been considerably altered by human influences, containing now often preponderantly balsam firs, we shall base our comparison mainly on the typical balsam woods, described by Kujala from the Gaspé Peninsula, and occurring also, for example, in Newfoundland and in central New Brunswick (Halliday, 1937).

Kujala (1945) divided them into at least 8 different forest vegetation types (Fig. 2). The balsam fir can be found in all 8 regions, but is dominant, and has its ecological optimum in two of them, named by Kujala the *Oxalis-Cornus*, and the *Oxalis-Dryopteris* type, respectively, the latter because of the abundance of ferns of the genus *Dryopteris*. Besides these two associations, the balsam may play an important role in the so-called *Aralia-Cornus* type, being somewhat more extreme (boreal), and furthermore in the highest developed and mildest *Mitella-Arisaema-Impatiens* type, an inhomogenous association apparently close to the white pine-hemlock formation of Halliday, in which balsam fir is associated under primaeval conditions with a number of deciduous trees, having become often dominant by human influences.

Each of these types is characterized by a certain group of typical plants, and among them we find a number of holarctic species, mainly mosses, ferns, grasses, and herbaceous plants, which live in Europe under ecologically restricted, and evidently similar environmental conditions. By a list of 27 such indicator plants (Table I), common on both sides of the Atlantic, we are able to outline the degree of correspondence between the Canadian balsam forests and the natural silver fir associations in middle Europe.

The greater part of these plants is regularly associated in Europe with the natural distribution area of the European spruce. In fact, *Picea abies* (= *P. excelsa*) must be

← Fig. 1. Winter temperatures and silver fir distribution in Europe. Average temperatures of January in Fahrenheit, in comparison to the values of Nova Scotia and New Brunswick. Dotted line: natural distribution of silver fir.

Fig. 2. Relationships between European silver fir associations and Eastern Canadian balsam fir forests. L, larch associations (*Rhodoreto-Vaccinietum*). P, subalpine spruce associations (*Piceetum*). A, Silver fir associations (*Abietetum*). AF, fir-beech associations (*Abieto-Fagetum*). F = beech associations (*Fagetum*). QC, Oak-hornbeam forests (*Querceto-Carpinetum*). NKCl, *Nemopanthes-Kalmia-Cladonia* type. KCl, *Kalmia-Cladonia* type. PKV, *Pleurozonium-Kalmia-Vaccinium* type. V, *Vaccinium canadense* type. ACo, *Aralia-Cornus* type. OCo, *Oxalis-Cornus* type. OD, *Oxalis-Dryopteris* type. MA, *Mitella-(Arisaema, Circaea, Impatiens, Filices)* type. PT, White Pine-Hemlock forests.



TABLE I — List of Indicator Plants, Present in Eastern Canadian Balsam Fir Forests and in European Silver Fir Woods.

	NKC1 PKV KC1	V	ACo	OCo (Canada)	OD	MA	LP P	PA	A (M. Europe)	AF	F	QC
<i>Empetrum nigrum</i>	—						+					
<i>Vaccinium vitis idaea</i>	++	+	—				++	+	—			
<i>Ptilium crista castr.</i>	++	++	++	++	+	—	++	++	++			
<i>Pyrola secunda</i>	—	+	++	—	—	—	++	++	++			
<i>Listera cordata</i>	—	—	++		—	—	++	++	—			
<i>Climaphila umbellata</i>		+	+				+	+	+	—		
<i>Corallorhiza trifida</i>		—	+			—	++	++	+	—		
<i>Polytrichum commune</i>		+	+	+			+	+	+	—		
<i>Pyrola chloracantha</i>			++				+	+	+			
<i>Goodyera repens</i>			++		—	—	++	++	+			
<i>Lycopodium annotin.</i>		—	+	++	+		++	++	+			
<i>Pyrola uniflora</i>		—		++	+	—	++	++	+			
<i>Equisetum silvatic.</i>		—	—	+				+	++	+		
<i>Rhytidiadelphus triqu.</i>		+	+	+	+	+	++	++	++	+	—	
<i>Hylocomium umbratum</i>			+	++	++	+	+	++	+			
<i>Oxalis acetosella</i>		—	+	++	++	+	+	++	++	++	++	—
<i>Dryopteris austriaca</i>			—	—	++	+	+	++	++	+	—	
" <i>filix mas</i>			—	+	++	+	—	—	+	++	+	+
" <i>phegopteris</i>			—	—	++	+	—	+	++	++	+	
" <i>linnaeana</i>			—		+	+	—	+	++	++	—	—
<i>Athyrium filix femina</i>				—	+	+	+	+	+	+	+	+
<i>Circaea alpina</i>					+	+		+	++	++	+	—
<i>Struthiopteris filic.</i>				—	—	+				—	+	+
<i>Mnium</i> spp.						+			+	++	++	++
<i>Geum rivale</i>						+			—	+	+	—
<i>Milium effusum</i>						+			—	++	++	—
<i>Climacium dendroides</i>						+				+	+	+

Distribution datas for Canada after Kujala (1945), for Europe after the standard literature on plant sociology.  
++ optimal occurrence, + regular occurrence, ÷ occurrence  
Abbreviations see Fig. 2

seen as the European counterpart of the balsam fir, while our European silver fir, *Abies alba* (= *A. pectinata*), as an Atlanto-Mediterranean element, belongs rather to the deciduous tree formation, and resembles ecologically more *Thuja occidentalis* L. or even *Tsuga canadensis* (L.) Carr. The silver fir occurs in the middle European mountains mainly in the so-called montane zone, that is between 2,700 and 4,500 ft. In the lower part of this region, up till about 3,500 ft., it is associated with beech, building up the so-called Abieto-Fagetum associations (AF in Fig. 2). In the uppermontane region and in the lowest parts of the subalpine zone, between 3,500 and 4,500 ft., *A. alba* is often absolutely dominant (A in Fig. 2). In the real subalpine region, above 3,500 ft. in the outer parts of the Alps, and above 4,500 ft. in the inneralpine parts, the silver fir becomes receding, and is replaced by the spruce (PA and P in Fig. 2). The latter is often associated with larch and stone-pines reaching to the timber line (L in Fig. 2).

As we have already emphasized, a remarkable part of the holarctic plants, very typical for Balsam forests of the *Oxalis-Cornus* and *Oxalis-Dryopteris*-type (OC and

OD in Fig. 2 and in Table I) are to be found in Europe mainly within the natural area of the spruce, *Picea abies* (L.) Karst., either in Northern Europe or in the subalpine girdle of the European mountains. Consequently we may conclude that those silver fir forests are more closely related to the optimal balsam woods in Eastern Canada, which border in Europe directly upon the spruce formation, in other words, the highest situated fir forests either of the typical uppermontane Abietetum-zone (A in Table I) or of the transition region between *Abies* and *Picea* (PA in Table I) at the lower subalpine elevations of the Alps. From a similar comparison of Table I it is to be seen that the closest allies of the balsam forests growing within the white-pine-hemlock formation are the natural beech-fir forests (AF) of the lowermontane zone of the middle European mountains. On the other hand, the fir forests most unsimilar to the balsam woods of Eastern Canada are to be seen in the afforestations of silver firs (often combined with spruce) within the oak-hornbeam formation (QC in Fig. 2 and Table I) of our lowlands and of the colline (hilly) zone, i.e. below elevations of 2,000 ft. Such artificially planted fir-spruce forests are widely distributed in Europe (as in middle and northern Germany, in the Swiss Middleland, in France, England, Sweden, etc., and they were in the past mainly subject of predator collections for importations into Canada.

How could we now prove that *Adelges* predators collected in the most similar European plant associations, i.e. in the natural fir forests at the uppermontane level of the Alps or Eastern European mountains, might be in fact more successful than others from less adequate biotops?

An indirect method would be the investigation of physiological or ecological tolerances by means of laboratory experiments, on the cold-hardness for example, with populations coming from different climatic regions in Europe, or from biotops with a different ecoclimate.

Probably more direct results may be obtained by the release of predator populations from different European origin in Canadian biotops, separated far enough to prevent interbreeding, but comparable in the status of the host infestation and in their biocoenotic structure. Such investigations may later make it possible to select specially adaptable European strains of useful insects.

With representatives of well marked groups (coccinellids, etc.), a third way might be accomplished by a careful study of the morphological variability of a predator species in different geographical regions of its original distribution area. The existence of geographic or ecological races, wellknown for certain coccinellids, for example, which are morphologically distinguishable, would then permit a simultaneous release of such different populations within the same area in Canada, and later to observe, which were able to persist and to compete most successfully under the new field conditions. This method should be completed by a similar study of the variability of the host, above all, by a comparison of the morphological status of the introduced population with the whole variability spectrum of the species in its natural area of distribution, with the intention of defining more closely the district from which the pest may have been imported, and to study especially the predator-prey complexes under these geographical and biocoenotic conditions.

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## DISCUSSION

A. E. BROWER. Did you say that *Adelges piceae* occurs in Switzerland up to 3500 feet and above?

H. PSCHORN-WALCHER. I did. A natural density of this species can be observed as high as 5000 feet; i.e. at the upper border of the fir distribution.



# *Adelges piceae* (Ratz.) in Canada with Reference to Biological Control<sup>1</sup>

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## ABSTRACT

The evidence regarding the identity and European origin of the balsam woolly aphid seems conclusive. It is destructive in Canada not only because the control complex is inadequate but also because *Abies balsamea* (L.) Mill. is very sensitive to its salivary injections — in contrast to *A. alba*.

In newly infested stands populations tend to rise rapidly on the stems of the more susceptible trees, which may be killed in a few years. Later they become more uniform and fluctuate less violently and at lower levels. They then cause more gradual but equally serious injury through effects on the twigs. To be fully effective biological control must regulate populations below the level causing twig injury.

The characteristics of an effective predator are discussed in relation to both types of attack. Ability to become established at low prey densities, and capacity to destroy the aphid before oviposition or hatching, are emphasized. 'Searching ability' in the larva is important, especially if number of prey consumed is large.

A complex of predator species with different ecological requirements will be most likely to maintain control in a variable environment. Native and introduced species are discussed with particular reference to dependence on high prey density.

Before undertaking any programme of biological control it is important to examine the evidence regarding the identity and origin of the pest concerned. It is also necessary to find out as much as possible about the factors of natural control already affecting it and why they are inadequate. The purpose of this paper is to review briefly what is known about *Adelges piceae* (Ratz.) in Canada, to discuss some questions that have arisen during the course of the work on introduction of natural enemies from Europe, and summarize progress to date.

## HISTORY

Evidence that the insect that has come to be known in Canada as the balsam woolly aphid was introduced from Europe, and is *Adelges piceae* (Ratz.), has been presented by Balch (1953). Its morphology and biology correspond with Marchal's (1913) description of *Dreyfusia piceae* Ratz. Pschorn-Walcher and Zwölfer (1956) have recently recognized two forms of *piceae*. Canadian material sent to Dr. L. P. Mesnil was identified as form *typica*. The closely related species *A. nüsslini* (Börner), with which it is frequently associated in Europe, has not been found in eastern Canada.

Since the insect causes formation of an abnormal type of wood in balsam fir, *Abies balsamea* (L.) Mill., it leaves a record of its infestation in the annual rings. This has provided evidence of its occurrence in western Nova Scotia about the beginning of the century. During the past fifty years or so it has spread throughout the Maritime Provinces, with the exception of the northwestern part of New Brunswick, and has reached Newfoundland. There is no winged stage capable of reproduction and the insect can spread only in the newly-hatched crawler stage, which experiments have shown can be carried considerable distances by wind. The spread has probably been retarded by the fact that it had to take place in the opposite direction to prevailing winds and storm tracks (Balch, 1952).

## NATURE OF DAMAGE

*A. piceae* causes little or no damage in Europe. Its destructiveness in Canada is due in part to inadequate natural control but also to the high susceptibility of the

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balsam fir to injury. The nature of the injury affects the need for biological control and determines the degree of control necessary.

In the forests of eastern Canada balsam fir is one of the two major tree species on which the pulpwood industry depends. It is the most prolific species and as our forests are managed on a basis of natural reproduction will always form a large, and probably increasing, component. In many areas, however, aphid attack has reduced it to the status of a 'weed tree'.

The common fir of Europe, *Abies pectinata* D. C., apparently suffers little even when heavily infested. Balsam fir on the other hand is very sensitive to the salivary injections of the aphid. It may be killed or severely stunted. This high susceptibility to injury was illustrated by plantings of a number of species of *Abies* at the Schovenhorst Arboretum in Holland, where *A. balsamea* and the closely related *A. fraseri* were badly damaged while all other species were thriving (Balch, 1953). The damage reported in Europe appears to be attributable to *nüsslini* rather than *piceae*. Kloft (1955) has suggested that the immunity of *A. pectinata* is due to formation of a secondary phellogen beneath the injured parenchyma, which protects the stem from continued attack, and that this enables the predators to destroy the remaining populations (see also Franz, 1956). *A. balsamea* also produces a secondary periderm but this often fails to protect the tree before the toxic effects of the insects' injections inhibit cambial or bud growth.

In discussing the behaviour of the insect and its effects on the tree it is convenient to use the terms 'stem attack' and 'twig attack'. It should be pointed out, however, that these are not two distinct types of attack, nor are they due to different forms of the insect. They serve only to describe stages and degrees of infestation and resulting contrasts in the distribution of the population on the tree and the type of damage.

'Stem attack' refers to heavy concentrations on the stem that are typical of recently infested stands and are generally found on the larger trees. The aphid often appears first, but not necessarily, on the lower part of the stems; it multiplies rapidly and tends to spread upwards. A good part of the stem may become more or less covered by the 'wax wool'.

In the first stages the annual ring is enlarged and consists of an abnormal type of wood, similar to 'rotholz'; later it is much reduced. Severe 'stem attacks' generally result in the death of the tree within 3 to 5 years of the first appearance of the insect. Some trees survive but these develop severe symptoms on the twigs, known as 'gout'.

'Twig attack' refers to lighter, persistent infestations in which the population may be distributed more or less uniformly over the stem and branches, but the damage is caused chiefly by the attack on the twigs. It is more characteristic of younger stands and stands that have been infested for a number of years.

The injury from 'twig attack' is gradual. It consists of swelling and distortion of new shoots and twigs, failure of bud growth, cessation of height growth, and dying of branches from the ends. The whole tree may die after some 10 to 25 years. It may eventually recover, more or less completely. In some cases this type of injury is more serious than death from 'stem attack' when the trees fail to reach merchantable size but continue to occupy growing space.

### ECOLOGICAL BASIS FOR BIOLOGICAL CONTROL

A brief résumé of what is known about the ecology of the aphid may help to indicate the basis for biological control, and whether the introduction of predators is likely to bring about the regulation of its populations at sufficiently low levels to prevent or reduce damage. Our studies have not been sufficiently lengthy or intensive to determine the exact role of the various components of what Thompson (1939) calls the "undissoluble complex" of influences determining populations. We can, however, give a general picture of the nature of the aphid population in Canada and the more evident mortality factors.

The aphid is thelytokous and bivoltine. Adults of the spring generation (or hiemosistentes) lay an average of roughly 100 eggs on favourable trees, those of the summer generation (or aestivosistentes) about 50. Thus a total mortality of from 98 to 99 per cent is necessary to prevent increase. There are no reproductive winged



forms and dispersal takes place only in the small, though active crawler stage. This is fairly rapid within the tree but slow and largely involuntary from tree to tree.

For some time after the insect first reaches an area this combination of high inherent capacity for increase and low dispersal capacity results in striking variations in population densities and trends between trees and between stands. Scattered 'stem attacks' appear, generally on the larger trees. Their location is determined partly by the chances of dispersal, partly by the favourableness of individual trees. Populations tend to rise rapidly on favourable trees until the tree is killed or develops resistance. When the tree dies the population is wiped out but a large 'surplus' of crawlers is generally produced prior to death. Some of these reach neighbouring trees, a few may be dispersed to greater distances by wind, but the great majority die.

When the insect has been present in an area for a number of years and the more susceptible trees have been killed, or have developed resistance as a result of attack, the stand becomes more uniformly infested; population densities become much lower and fluctuate less violently. 'Twig attack' tends to replace 'stem attack'.

This general picture is varied by the varying interacting effects of weather and other factors (Balch, 1952). An important climatic factor is low winter temperature. Mortality is generally high during the winter and occasionally reaches 100 per cent above snow. Rain and direct sunlight cause mortality during the summer. Also summer temperatures affect the number of overwintering larvae produced by the summer generation. There are always some adults that develop too late to complete oviposition, and a number of eggs that fail to hatch before winter sets in. In cool summers this limitation of the reproductive rate may be important, especially near the coast and at higher elevations. Thus climatic factors have caused regional reductions of populations and have influenced the rate and timing of increase and spread. They have not, however, prevented populations eventually reaching tree-killing level.

The percentage mortality caused by climatic factors is directly related to density only in the case of rain and sunlight, when an increasing proportion of the population occupies less protected sites as a tree becomes heavily infested. In the long run populations have been limited by the more clearly density-related biotic or non-climatic factors, although their effects are, of course, influenced by weather. These may be considered under tree resistance, with its effects on fecundity and survival; mortality from starvation and dispersal; and predation.

The rate at which a population rises and the ultimate level reached on a tree are influenced by the tree's external and internal characteristics. As already mentioned, trees vary in the protection they afford from weather. Also the fecundity of the adult aphids and the proportion of the larvae surviving diapause vary from tree to tree and there is evidence that this is due to variation in the quality of the tree, or parts of the tree, as food. At the same time trees vary in their ability to produce a secondary periderm during attack and thus reduce the area available for feeding. These qualities that limit reproduction and survival are considered as 'tree resistance'. Their effect increases within a stand as the less resistant trees are killed or develop resistance. In the absence of other regulating factors the degree of resistance determines the upper limit of the population on a tree or in a stand.

Mortality from dispersal and starvation is high in the late stages of 'stem attack', particularly when the tree dies. The generation that develops just prior to the death of the tree generally produces a large number of crawlers. Some of these settle on unoccupied bark which dies before they are able to feed. The majority disperse from the tree but fail to reach a suitable host.

The only natural enemies are insect predators. No parasites or diseases have been found attacking the Adelginae.<sup>5</sup> Eighteen native species of insects and mites have been observed feeding on the aphid in Canada, most of them only occasionally (Brown and Clark, 1956b). A few become numerous at times in heavy populations on the stem. Little is known about the alternative hosts of the native predators. With the possible exception of *Leucopina americana* (Mall.) and one or two syrphids, none appears to have a strong preference for *A. piceae* or to be capable of destroying a significant

<sup>5</sup>Fungi found in Europe and Canada appear to be more saprophagous than parasitic (Schremmer, 1956).

number of the aphid until it has become numerous enough to cause severe damage to the tree. Although these species are "density-related" it is the density of the prey that determines the numbers of the predators rather than the predators that determine the density of the prey.

The following conclusions are drawn from what is known of the ecology of the insect in the Maritime Provinces. The climate is sufficiently favourable to permit its rapid increase in a normal year. Climatic factors have been responsible for periodic regional reductions in populations but have seldom prevented increase in the summer generation. Although weather has influenced the rate of growth and spread of populations, the population level in a stand has ultimately been determined by the degree of 'tree resistance'. Native predators have become well established only at high densities of the aphid and have destroyed only a part of the population in excess of that necessary to kill or damage the trees.

Stand resistance may be increased to some extent by the removal of the trees of merchantable size but even this apparently simple expedient is not always practicable under present conditions of forest management in Canada, nor will it prevent injury to immature stands. The evident need is for natural control factors that are directly density-related and are capable of reducing populations before they reach the levels at which trees are killed or severely injured. The only hope of this seems to lie in the introduction of more effective predators.

The prevention of injury by 'twig attack' will call for regulation at a considerably lower level than the prevention of killing by 'stem attack'. The latter alone will be of considerable value; it will reduce and delay the mortality of trees and by checking dispersal will reduce the rate of spread. If, however, predators cannot be established that will control 'twig attack', 'gout' will continue to be prevalent.

#### CHOICE OF SPECIES FOR INTRODUCTION

Since the Biological Control Unit of the Division of Entomology and the Commonwealth Bureau of Biological Control commenced work on this project a considerable number of species of predators have been recorded as feeding on *A. piceae* in Europe (Pschorn-Walcher and Zwölfer, 1956). The problem would be simplified if we knew beforehand which would be effective in Canada. This is not possible. Any attempt to determine even the probabilities would delay introductions indefinitely. It would involve exhaustive ecological and population studies on both continents and the conclusions would be of dubious value until tested on this continent.

The choice of species for introduction has been determined to a considerable extent by ease of collection. This tends to select those that are most numerous at high densities of the prey, although not necessarily those that are most effective in maintaining low densities. The policy seems justified in the first stages of the programme but the ultimate objective should be to test by actual introduction as many species as possible.

Following the reasoning of Smith (1929) and Thompson (1939) there would seem to be little likelihood of prejudicing the success of biological control by the introduction of a number of species. The "mixed species problem" has been discussed by Allee *et al.* (1949). Experiments with laboratory populations indicate that a more effective predator will exterminate a less effective predator when they occupy identical niches. This would seldom occur in natural populations in the forest owing to the temporal and spatial variations of the environment and the rarity of ecologically equivalent species. The ecological requirements of predators of the aphid overlap but will nearly always vary in some particular. Competition may result in the extermination of a less aggressive species on individual trees but its power of dispersal to other trees in a different stage of infestation would probably ensure its survival. It was found, for instance, that when *Neoleucopis obscura* (Hal.) first became abundant in Canada the native *Leucopina americana* (Mall.) became relatively scarce but did not disappear. In any case the total predation is not likely to be decreased by competition between species.

The distribution of the aphid covers a considerable range of climatic conditions. The microclimate varies also on different parts of a tree. Extreme variations in its

population density add to the variety of environmental conditions within which the predator complex must operate. The larger the number of species in the complex the greater the chances that it will regulate the population of the prey with some degree of constancy in a varied and changing environment.

To give a simple example. If the numbers of one predator that overwinters on the bark are reduced by an unusually severe winter, its place may be taken by another species that would otherwise be less able to compete but is more resistant to low temperature or overwinters beneath the snow.

Predators also vary in their ability to become established at different prey densities. Some will be effective only on 'stem attacks'; others may be capable of preying on the more scattered populations on the twigs. They may be favoured by the ecological conditions on one or other of these parts of the tree. Different species, or groups of species, will probably be effective at different densities. There is considerable evidence that this is so with parasites of the spruce sawfly (Reeks, 1953) and the spruce budworm Morris *et al.*, 1956).

The probable compensating effects of a large complex of predators seem to justify the introduction of all available species. Their ultimate role can be determined only by subsequent study in the areas of introduction. The policy has been to make liberations first in central New Brunswick, where 'stem attacks' are most common, using cages with the first colonies. If a species becomes well established further liberations are made at distances of fifty or more miles. Three species have been liberated in Newfoundland. If failure to become established seems to be due to low winter temperatures, further liberations may be made in milder climatic zones near the coast.

After a species has been given an adequate opportunity to become established in central New Brunswick, at points near the coast, and in Newfoundland, further introductions seem unjustified. If, however, it shows some capacity for improving control its distribution throughout the area of aphid infestation may be hastened by additional liberations at widely separated localities. It may be some years before the value of a species can be assessed. Clausen (1951) has concluded from the history of biological control that a "fully effective" parasite or predator will demonstrate its value at the point of introduction within three years or less. He referred, however, to species capable by themselves of giving complete and permanent commercial control and, as Thompson (1951) has pointed out, did not envisage the building up of a complex of species. Nor did he seem to recognize the value of partial control, which is likely to be greater in forestry than in agriculture.

It may be mentioned, however, that Clausen's ideas as elaborated by Thompson receive some support from the behaviour of *N. obscura*. This predator demonstrated its capacity to produce high populations on heavy 'stem attacks' at the point of liberation within a year of its introduction, although its control value was limited by factors mentioned below.

### CHARACTERISTICS OF AN EFFECTIVE PREDATOR

Although the value of a predator can best be determined by introduction it is desirable to consider what are the characteristics of a predator that are likely to make for its success in this case. This should help to determine which species are most likely to warrant the cost of introduction and should be given priority. It will also indicate certain characteristics that are worthy of study so that we may discover reasons for success or failure.

**ADAPTABILITY TO CLIMATE:** An obvious necessity is the capacity to survive climatic conditions in Canada. The most severe test is likely to be the long, cold winter. Species that overwinter on the bark must withstand temperatures as low as  $-25^{\circ}\text{F}$ . if they are to survive an average winter at Fredericton, N.B., and  $-32^{\circ}\text{F}$ . if they are to become permanently established. Those that winter in the ground will seldom experience temperatures much below  $15^{\circ}\text{F}$ . but must be able to survive ice formation, which occurs commonly around the base of trees, and also waterlogged conditions in the spring.

Species that normally overwinter on the bark may also be found in small numbers in the forest floor, or be protected by snow on the base of the stems — *N. obscura* for example. Thus a predator may survive in small numbers in protected sites. To be effective, however, it must have a low mortality rate (see Varley, 1953) and its susceptibility to mortality from climatic factors should not be greater than that of the aphid. Species or races found in northern Europe are most likely to possess this qualification.

**SYNCHRONOUS LIFE HISTORY:** The seasonal life history and phenology should be so related to the aphid that the feeding stages of the predator are active when the vulnerable stages of the prey are most numerous. One stage, the dormant neosistens, occurs throughout the year but is seldom if ever attacked by predators. A number of predators will feed on the crawler but we have observed relatively little predation on this stage, although Pschorn-Walcher and Zwölfer (1956) indicate that it is attacked by most species in Europe. In Canada most predators feed on the second, third, and adult stages, on the egg, or on all four.

One aspect of the synchronization of development is of particular importance. Destruction of adults after oviposition is well advanced will have little or no control value, unless the eggs are also destroyed. The most effective predator will be one that commences feeding soon after the aphid begins to develop in the spring, and reaches the mature larval stage before the adults commence ovipositing. Thus it will be able to make the maximum use of the available food, which is important if it is to maintain itself at low levels of population, and at the same time exert the maximum regulating effect on the numbers of the second generation. An example will be given below in a comparison of the feeding habits of *N. obscura* and *Laricobius erichsonii* Rosen.

Other things being equal, a predator with two generations per year synchronized with the two generations of the aphid should be more effective than a univoltine species. The stages fed on, however, may be more important than the number of generations.

It should be noted that increases in the aphid populations normally take place in the summer generation. This is because the overwintering larvae of the spring generation suffer high mortality and the adults have a higher fecundity than those of the summer generation. A larger number of predators is therefore necessary to prevent increase when the attack is on the summer generation. A given percentage of predation, however, will have the same effect on annual population trend regardless of the generation in which it occurs. It might appear that a predator attacking only the spring generation would be more effective than one attacking only the summer generation. On the other hand, given equal searching ability, the latter would become established at an earlier stage in an infestation and have an equal opportunity to produce the numbers necessary for control at the same level of prey population.

**FECUNDITY:** The innate capacity of a species to multiply is a function of the number of generations per year and its fecundity. It cannot be expressed quantitatively except for a particular environment (see Andrewartha and Birch, 1954). An introduced predator will not necessarily have the same number of generations or lay the same number of viable eggs per average female in Canada as in Europe. Fecundity has not generally been considered to limit the abundance of a species and, perhaps for this reason, it has not been studied for any of the predators of the aphid. Smith (1939) has stressed the relative unimportance of inherent reproductive capacity in parasites. It may be less important in the case of predators since the number of eggs necessary for control is smaller in proportion to the number of prey consumed by the individual predator.

When environmental conditions, including the density of prey, are optimum, fecundity and number of synchronized generations may determine the rate at which a predator multiplies. In the case of 'stem attacks' this could decide its capacity to control the population before the tree is killed. However, its ability to discover infested trees and become established at low prey densities seems to be of more importance.

**SEARCHING ABILITY:** The ability of an entomophagous insect to find its prey under varying conditions of density and distribution is of prime importance in de-



termining the level at which it can achieve control. This has been discussed by a number of authors concerned with theories of population dynamics (Nicholson, 1933; Smith, 1939; Thompson, 1939; Varley, 1946; Andrewartha and Birch, 1954; Schwerdtfeger, 1950; Solomon, 1949).

Nicholson and Bailey (1935) have presented a formula for calculating the "area of discovery" when the density of the predator population and the proportion of prey destroyed are known. This is considered to be a measure of the effectiveness of the predator in discovering and destroying its prey. Varley applied the formula to field data and suggested that the results supported the theory on which it is founded. The assumption that the area of discovery is independent of predator and prey density is open to criticism (Andrewartha and Birch, 1954). It may, however, be a useful statistic and its value should be tested in studies of natural populations. Unfortunately it is more difficult to measure with predators than with parasites. They do not leave as clear evidence of the percentage of the prey that has been destroyed.

We use the term "searching ability" to describe the inherent capacity of the average individual of a species to discover enough food to complete its development. It consists of the combined powers of locomotion and perception and the ability to consume the stages of the prey that are present. Insect parasites search only in the adult stage; predators must search in both the adult and the larval stages. Not only must the winged adult be able to discover new infestations or colonies of its prey, in which to lay its eggs, but the wingless larva must cover a sufficient area to obtain the number of prey necessary to complete its development (Smith, 1937).

The dispersive power of the predator must equal the dispersive power of the aphid. Since the aphid has no winged stage capable of reproduction, and is dispersed any distance only by the fortuitous transportation of the crawler, predators do not seem likely to be limited by searching ability in the adult stage. The rapidity with which *N. obscura* became established throughout the range of the aphid (Brown, 1947) illustrates this. The wandering habit of the crawler, however, causes it to become rapidly dispersed on individual trees so that the offspring from one egg mass tend to be widely scattered. Thus at low levels of prey population the searching ability of a predator in the larval stage may be the limiting factor in its survival. This appears to be the chief reason why *N. obscura*, and other predators, become established only after the aphid population reaches a fairly high level. Because of the relatively sluggish habits and large 'appetite' of the larva they belong to the group of predators that can maintain a low "steady density" only when their prey is strongly colonial in habit. Although 'stem attacks' represent a strongly colonial type of distribution within a stand, the distribution of the aphid on individual trees is more or less uniform and non-colonial.

Predators of this type are particularly handicapped in their ability to control 'twig attack', when the aphid is scattered in relatively small numbers over shoots, twigs, and branches. If the predacious larva is to find its requisite number of prey it must travel much longer distances (have a greater "areal range") than when the aphid occurs on the relatively flat and continuous surface of the stem, even if the population per surface area is the same. As the number per surface area that is necessary to cause damage is less on the twigs than on the stem, control must take place at a lower level of population. Thus searching ability is of great importance for the control of 'twig attack' and the prevention of 'gout'.

'APPETITE': Searching ability cannot be considered apart from the number of prey needed by the individual predator to complete its development. This is referred to as its 'appetite'.

References in the literature frequently emphasize the "voraciousness" of a predator as evidence of its value. At given population densities the larger the number of prey destroyed per predator the greater will be the percentage mortality and the greater the reduction of the prey population in any one generation. A species with a large 'appetite', however, must have a proportionately large "areal range" if it is to survive. If it is relatively sluggish in the larval stages it will not become established at low prey density and its 'appetite' may limit its value.



The native predators that have been found attacking *A. piceae* in any numbers seldom if ever occur except on moderately heavy to heavy 'stem attacks'. Most of them are Diptera. In the adult stage they apparently have high searching ability but do not feed. In the larval stage they are rather slow-moving and have a large 'appetite'. Dependence of the larva on a large number of prey in a relatively small area seems to be a major factor limiting their capacity to become established at low prey density.

As parasitic larvae need only one host to complete development insect parasites need searching ability only in the adult stage. It would appear therefore that parasites as a class tend to be better fitted to control non-colonial types of insects at low densities, although predators are better fitted for rapid control at high densities (Flanders, 1947).

If this is so, the less voracious a predator the more nearly will it approach the parasite in its capacity to control light scattered populations. A small 'appetite', if combined with good searching ability in the adult stage and the other necessary characteristics of an effective predator, would increase its effectiveness against 'twig attack'. This is one reason why the European *Aphidoletes thompsoni* Möhn, a small fly, seems to be a desirable introduction. An egg predator capable of developing on a single mass would be valuable.

**SPECIFICITY:** The effectiveness of a predator will be influenced by the number of species on which it feeds. Some authors have suggested that predators are less effective than parasites because they are more polyphagous. Many, however, are strongly specialized in their food requirements, although it is doubtful if any are strictly "specific". We have found for instance that *Chilocorus stigma* Say seldom fails to attack infestations of the beech scale, *Cryptococcus fagi* (Baer.), but attacks the balsam woolly aphid only very occasionally, even when both species of prey are present in large numbers in the same stand.

A predator is most likely to be effective against a species for which it has a strong preference. At the same time ability to feed on other species that occur in the same environment will increase its chances of survival if the preferred host becomes scarce. Alternative aphid prey species are, however, uncommon on balsam fir, with the exception of *Mindarus abietinus* Koch. This is periodically abundant but occurs only on the twigs. Aphids occur on trees associated with balsam fir but generally only in small numbers. Ability to feed on other species may therefore have limited value.

Obviously the native predators are not specific to *A. piceae*, but little is known of their alternative prey species. None appears to have developed a preference for *piceae* with the possible exception of *Leucopina americana* (Mall.) and one or two species of syrphid, which sometimes become numerous. No definite records have yet been obtained of the European predators feeding on other species in the forest.

### STUDIES OF INTRODUCED SPECIES

Between the years 1933 and 1941 colonies of the following species were liberated in New Brunswick. *Neoleucopis obscura* (Hal.) ('33, '34, '35); *Lipoleucopis praecox* de Meij. ('33); *Hemerobius stigma* (Steph.) ('35, '37, '38); *Hemerobius nitidulus* Fabr. ('35); *Exochomus quadripustulatus* L. ('36, '37, '39, '40); and *Aphidecta oblitterata* L. ('41). Of these only *N. obscura* has been recovered.

The project was revived in 1950 and further introductions were made through the co-operation of the Biological Control Unit of the Division of Entomology and the Imperial Institute of Biological Control (Smith and Coppel, 1957). Releases are summarized in Table I.

The work leading up to these releases will be discussed by other contributors to the symposium. Our studies have been concerned with populations in the field subsequent to release. A system of sampling the populations of the aphid and the predators on measured areas of bark surface has been employed. The following notes briefly summarize a few general conclusions arrived at to date.

Neoleucopis obscura

This chamaemyiid fly provided a striking example of rapid establishment and spread. It soon outnumbered all native predators, which it tended to replace, and within 14 years spread throughout the infested area in the Maritime Provinces (Brown, 1947). There has been some reduction in its numbers during the past few years but it is still the most generally occurring predator.

TABLE I — Summary of Liberations of Predators from Europe 1951-1955.

		1951	1952	1953	1954	1955
<i>Laricobius erichsonii</i> (Rosen.)	N. B.	2,177	2,721	9,122	8,629	—
	N. S.	—	—	—	112	870
	Nfld.	—	843	—	2,502	5,424
<i>Pullus impexus</i> (Muls.)	N. B.	3,572	7,864	11,863	16,023	—
	N. S.	—	2,139	—	—	120
	Nfld.	—	1,306	1,534	4,570	890
<i>Aphidecta oblitterata</i> L.	N. B.	271	2,035	—	—	214
<i>Cremifania nigrocellulata</i> Cz.	N. B.	—	676	1,082	3,329	81
<i>Neocnemodon</i> spp.	N. B.	—	—	—	703	—
<i>Aphidoletes thompsoni</i> Möhn	N. B.	—	—	—	—	36
<i>Neoleucopis obscura</i> (Hal.)	Nfld. (from N.B.)	—	—	—	—	21

It has high searching ability in the non-feeding adult stage and two generations well synchronized with the aphid for its own survival. Winter mortality is sometimes high but not much greater than that of the aphid. Parasitism by *Pachyneuron altiscutum* How. sometimes regulates its numbers.

It has been found only on fairly heavily infested stems and is evidently dependent on high prey density. This limitation is associated with the restricted searching ability and large 'appetite' of the larva. Also it feeds too late in the developmental periods of both generations of the aphid to provide an efficient control of oviposition, feeding as it does quite largely on adults that have already laid many eggs rather than on the immature stages and eggs. Its regulating effect does not appear until after the aphid population has reached a level at which the tree is killed, or severely injured. It does, however, check the rise of aphid population in the late stage of 'stem attack' and reduce the number of surplus crawlers disseminated at this stage.

Since the establishment of this predator extremely heavy stem infestations, completely covering the bark with 'wool', have become rare. Attacks, however, have continued with sufficient severity to kill trees. The rate of spread has also declined in New Brunswick. *N. obscura* has undoubtedly played a part in this, but its exact importance is not known.

Laricobius erichsonii

This derodontid beetle has become well established near Fredericton and is known to have spread distances up to 2 miles. Its somewhat slower spread is explained in part by its univoltine habit, and probably by the less active flight habits of the adult. There is some overwintering mortality but as it hibernates in the ground the extreme low temperatures do not affect it.

Its development is well synchronized with that of the spring generation of the aphid. The adults, which overwinter, commence feeding on the immature stages. The larvae feed first on eggs and later on adults and remaining younger stages; they are fairly active searchers. The spring generation has sometimes been almost completely destroyed at points of liberation. In 1955 and 1956 natural populations at some distance from liberation points have also shown the ability to terminate 'stem attacks'.

This species promises to improve the control of 'stem attack', but it has been found only occasionally on light infestations. Its searching ability in the larval stage appears insufficient for its survival on twig infestations and may limit its value in the prevention of 'gout'.

*Pullus impexus*

This rather small coccinellid became established at most liberation points and has spread short distances. It has survived five seasons. It overwinters as an egg on the bark and the larvae feed on the second and third stages, on adults and eggs. Later the adults feed on the same stages. Thus its seasonal history appears favourable to controlling the spring generation.

Populations have remained small but we do not know what has limited its increase. Winter mortality may be high and this would be of particular importance with a univoltine species. Also, the adults often occur between aphid generations when only the dormant neosistens is present, and it does not appear to feed on this stage.

*Cremifania nigrocellulata*

Establishment of this chamaemyiid has resulted at all release points but its maximum recorded spread is  $\frac{3}{4}$  mile. Although fairly large numbers have developed on some stem infestations it has been less numerous than *L. erichsonii* or *N. obscura*.

There are two generations per year. It overwinters in the puparium, mostly in the ground but also on the bark. The first generation larvae commence feeding slightly earlier than *N. obscura* but later than *L. erichsonii* and do not seem able to prevent considerable oviposition and hatching. They are fairly active but have not been found on light infestations. The second generation is small, apparently owing to diapause in the first generation.

Little is known of control factors. Some parasitism by *Pachyneuron altiscutum* has been recorded by Brown and Clark (1956a). The species appears to be a useful addition to the control complex but it is too early to assess its value.

*Aphidecta oblitterata*

Four attempts have been made to introduce this coccinellid. All stages have been recovered during the year of release but none in the following year. A further attempt at establishment is being made with material from Sweden.

This species has one generation per year. It overwinters as an adult in the ground but apparently does not survive our winter. It is reported as feeding commonly on twigs in Europe—presumably on *A. nüsslini*—and seems to be polyphagous. The adult and larva should have good searching ability and it is desirable to give it as good an opportunity as possible to become established. Possibly there are races in northern Europe that will be better adapted to our climate.

*Aphidoletes thompsoni*

This small, delicate fly has proved difficult to handle. A very weak colony was caged in the field but produced no offspring. Apparently it is sometimes numerous in Europe. Its small size and presumably similar 'appetite' suggest that it may be capable of surviving on light infestations and reducing 'twig attack'. Continued efforts to solve the problems of rearing and shipping are justified.

*Neocnemodon* spp.

Several small shipments were liberated in 1954. No evidence of oviposition was obtained and no recoveries have been made.

The results to date may be summarized briefly. Four species are well established. *N. obscura* has multiplied rapidly and spread widely but reduces the aphid population only in the later stages of 'stem attack'. It has not prevented the killing of trees but may delay their death and has helped to check spread. *L. erichsonii* has shown the ability to reduce 'stem attacks' sharply before the tree is killed. It commences feeding earlier in the spring than other abundant species and can destroy most of the immature stages and adults and consume the eggs before they hatch. This gives it an advantage in competition. It is too early to determine its ultimate value. *P. impexus* and *C. nigro-*

*cellulata* have so far multiplied and spread only very slowly and their value is uncertain. An important lack in the predator complex is a species capable of attacking light infestations and preventing 'gout'.

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# Predators of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) (Homoptera: Phylloxeridae) Recently Introduced into Canada<sup>1</sup>

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## ABSTRACT

Four of 11 species of insect predators introduced from Europe and released against *Adelges piceae* (Ratz.) in Eastern Canada from 1933 to 1955 have been recovered. *Neoleucopis obscura* (Hal.) is established over most of the area occupied by *A. piceae*. *Cremifania nigrocellulata* Cz., *Laricobius erichsonii* Rosenh., and *Pullus impexus* (Muls.) are established in the vicinity of Fredericton, New Brunswick. Progeny of *Aphidecta oblitterata* (L.) were first recovered at Fredericton in 1955. *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* appear relatively specialized, and *A. oblitterata* is less specialized in relation to species of prey attacked. The larvae of these species do not regularly attack the first-instar larva of *A. piceae*, and at high prey densities they must first eliminate the surplus population before prey survival is affected. Both the last-instar larvae and adults are active over relatively wide ranges of air temperature.

## INTRODUCTION

Details of releases and reviews of bionomics in Europe of insect predators of the balsam woolly aphid, *Adelges piceae* (Ratz.), will be published (Smith and Coppel, in preparation). The importations occurred in two phases, the first of which began in 1933 and the second in 1951. The species released in the first phase were *Aphidecta oblitterata* (L.) and *Exochomus quadripustulatus* L. (Coleoptera: Coccinellidae), *Hemerobius nitidulus* Fabr. and *Hemerobius stigma* Steph. (Neuroptera: Hemerobiidae), and *Neoleucopis obscura* (Hal.) and *Lipoleucopis praecox* de Meij. (Diptera: Chamaemyiidae). Of these *N. obscura* is the only species that was recovered. This species has not given adequate control though it has become established throughout most of the area occupied by *A. piceae* (Balch, 1952). The species released in the second phase were *A. oblitterata* and *Pullus impexus* (Muls.) (Coleoptera: Coccinellidae), *Aphidoletes thompsoni* Moehn (Diptera: Cecidomyiidae), *Cremifania nigrocellulata* Cz. (Diptera: Chamaemyiidae), *Laricobius erichsonii* Rosenh. (Coleoptera: Derodontidae), and *Cnemodon pubescens* Delucchi and Pschorn-W. (Diptera: Syrphidae). *C. nigrocellulata* was recovered in 1953, 1954, and 1955, and *L. erichsonii* and *P. impexus* in 1952, 1953, 1954, and 1955 in the vicinity of Fredericton, New Brunswick. Progeny of *A. oblitterata* were first recovered from releases made in 1955, but it is not yet known whether this species is established. The purpose of the present paper is to review briefly the work of the Belleville laboratory on the bionomics of *N. obscura* and species recovered since 1951.

## FEEDING HABITS

With the exception of *A. oblitterata*, the predatory species appear to be relatively specialized in relation to prey attacked, and the preferred prey are probably restricted to the genus *Adelges*. *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* were not observed to attack any stage of the aphid *Myzus persicae* Sulzer or the mealy bug *Pseudococcus* sp. under laboratory conditions. *A. oblitterata* is less specialized than the other predators in regard to species of prey attacked. In the field, last-instar larvae of this species were found on infestations of the aphid *Mindarus abietinus* Kock. *A. oblitterata* was reared from egg to adult on the nymphs and adults of this species in the laboratory. Adults of *A. oblitterata* were observed to attack the nymphs and adults of *Macrosiphum ambrosiae* Thomas and *Periphyelus populicolus* Thomas in the laboratory, but were not recovered from infestations of these aphids in the field.

Adults of *A. oblitterata*, *L. erichsonii*, and *P. impexus* are predatory but rarely attack the first-instar larva of *A. piceae*. *A. oblitterata* adults were observed to attack the crawler or motile form occasionally, and in the absence of the other prey stages

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adults of *P. impexus* were observed to attack the sessile form. Adults of *L. erichsonii* were not observed to attack either form of the prey first-instar larva. Though the observed rates of prey destruction by individual adults of the three species are comparatively high, the adult stages may not be of significance in control as large numbers are not found in the field.

With the exception of the fourth-instar larva of *A. obliterated*, the larva of *A. obliterated*, *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* were not observed to attack the first-instar larva of *A. piceae*. The fourth-instar larva of *A. obliterated* was observed to attack the crawler occasionally. All other prey stages are attacked by the larvae of the four predatory species, but prey wax and integuments are not ingested. The last-instar larva of each predator destroys more than 50 per cent of the total prey destroyed by all instars of each species. It is probable that the last-instar larvae are the most important stages from a control point of view. The control value of the last-instars is, however, limited because they do not attack all stages of the prey.

### PREDATOR-PREY INTERACTIONS

The development of predators was observed in field cages, and studies of the influence of predator populations on the survival of *A. piceae* were made (Smith, in preparation, a). Control investigations on prey survival were conducted in conjunction with the studies of predator-prey interaction. Changes in second generation, or aestivosistens, populations of the prey exposed to predation in the first, or hiemosistens, generation were compared with changes in aestivosistens populations that developed from predator free hiemosistens populations. Amount of predation by larvae of the predators was expressed in terms of larva-days. Censures of prey adults and second and third-instar larvae were made for both hiemosistens and aestivosistens populations.

At high prey density, 1,487 larva-days of *A. obliterated* from May 26 to July 4, 1,232 larva-days of *C. nigrocellulata* from June 17 to June 28, and 836 larva-days of *L. erichsonii* from June 17 to July 7 reduced prey survival by approximately 81, 70, and 76 per cent respectively. At low prey density, 652 larva-days of *L. erichsonii* from June 12 to July 4 reduced prey survival, whereas, at high prey density, 896 larva-days of the same species from June 25 to July 20 failed to reduce prey survival. The predatory larvae occurred before the crawler and sessile first-instar prey larva became abundant in all interactions except the last. The time of occurrence of the predators with respect to the prey stages is a factor of considerable importance in control because the predators do not attack the first-instar prey larva.

The level of prey density that will result after the introduced species have reached equilibrium in the complex will depend to a large extent on the feeding characteristics of the predatory species. The fact that the larvae of *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* do not attack either the crawler or the sessile first-instar larva of the prey and that *A. obliterated* larvae attack the crawler only occasionally is of particular significance. The crawler is the only motile form of the prey, and the sessile first-instar larva is present throughout the year. Competition between the stages of the prey is severe at high population densities, and relatively few progeny of the hiemosistens reach the adult stage. A large surplus population that provides subsistence for predators is produced. Consequently at high prey density the predators must first eliminate the surplus population before prey survival is affected. The chances of the larvae of *A. obliterated*, *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* accomplishing this are greater when they are present before the first-instar prey larvae become abundant.

### INFLUENCE OF LIGHT AND TEMPERATURE ON ACTIVITY

Observations on individual adults of the predatory species and on groups of at least 25 last-instar larvae were made in the field under various conditions of light and temperature, and attempts were made under laboratory conditions to compare the responses to light and the influence of light and temperature on locomotion of adults. The methods and equipment employed in these investigations are described elsewhere (Smith, in preparation, b).

In a temperature range of 15°C. to 25°C adults of *C. nigrocellulata* and *N. obscura* were seen to be active during the day and were attracted to areas of

sunlight. The activity consisted of short flights. Adults of *A. obliterated*, *L. erichsonii*, and *P. impexus* were not often seen in flight, but were usually found stationary or walking on the bark surfaces. These species were observed to walk in a temperature range of from 8°C. to 25°C., and did not appear to be strongly attracted to light. Newly emerged adults of these species avoided light of high intensity, whereas actively feeding adults confined to small darkened cages were attracted to perforations in the cage covers through which some light entered. In the field the larvae of *C. nigrocellulata* and *L. erichsonii* showed little tendency to leave areas in which they were feeding as long as adequate food was present. The larvae of *P. impexus* showed a preference for the uppermost bark areas, whereas those of *A. obliterated* distributed themselves randomly. None of the species showed a preference for areas where the prey density was highest and all species fed during the hours of darkness. Changes in air temperature did not greatly influence the activity of the larvae. The average proportions of larvae of *A. obliterated*, *C. nigrocellulata*, *L. erichsonii*, and *P. impexus* in movement at any one time were 45, 15, 30, and 45, and average distances moved per 30 minutes were 3.12, 1.67, 1.36, and 5.33 cm. respectively. The former figures are average per cents and the latter the estimated minimum displacements based on observations made between 9:00 a.m. and 7:00 p.m.

The results of laboratory tests on the light responses of adults confirmed results of field observations on *N. obscura* and provided a better understanding of the light relations of the other species. *N. obscura* is strongly attracted to direct light at temperatures of 12°C. and 25°C., indifferent at approximately 36°C., and repelled at a temperature of 37°C. *A. obliterated* is attracted to direct light, whereas *L. erichsonii* and *P. impexus*, though not attracted to direct light sources, are attracted to indirect low intensity light. Present evidence indicates that in order of light tolerance of adults the arrangement of species is *N. obscura*, *A. obliterated*, *P. impexus*, and *L. erichsonii*. The frequency of path-crossing was greater for all species at low light intensity than at high indicating that more new area is covered at high light intensity.

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## DISCUSSION

G. C. VARLEY. Although the large *Aphidecta* larvae kill more *Adelges*, is not the critical stage in the life-history of *Aphidecta* the 1st stage larva and the oviposition responses of the beetle?

B. C. SMITH. If the 4th stage larva of *A. obliterated* occurs before the immune stages of *A. piceae* occur, the 4th stage larva will be more important from a control point of view.



# The Present Status of the Balsam Woolly Aphid in the United States

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## ABSTRACT

Balsam fir suffers heavy mortality from the balsam woolly aphid in Maine, New Hampshire and Vermont. Surveys on the Green Mountain National Forest in 1956 indicate about 75 percent of the merchantable volume is infested on the affected areas and that 21 percent of the merchantable volume has been killed within the last 5 years. Comparable figures for affected areas on the White Mountain National Forest are 50 percent of the trees infested and 8 percent killed. In Maine trunk attack has killed much of the older fir in Washington and Hancock Counties and the annual loss in affected areas probably runs from 10 to 20 percent. On the coast the gout type of injury is most prevalent and infested trees rarely reach merchantable size.

The important predator, *Leucopis obscura* Hal., has spread naturally from New Brunswick throughout Maine. It is now being colonized in the rest of the region. Colonies of *Pullus impexus* Muls. and *Laricobius erichsonii* Rosenh. were released in 1955, and *Laricobius* has been recovered in southern Vermont.

The pest has been killing grand fir in the Willamette Valley of Oregon since about 1930. Surveys in 1954 and 1955 showed serious infestations on silver fir in both Oregon and Washington. Almost 300,000 acres are affected with about 57,000 heavily infested.

With the possible exception of the spruce budworm, the balsam woolly aphid, *Chermes piceae* Ratz., is the most destructive insect pest of balsam fir (*Abies balsamea* (L.) Mill.) in the northeastern part of the United States. Nevertheless, there is little factual data available from the region regarding annual tree mortality or loss in volume caused by the insect.

In view of the fact that Canada is pursuing an energetic program of importing predaceous enemies of the aphid, from which we are benefitting very materially, this would seem to be a logical time to appraise the seriousness of aphid damage in the United States and also to consider the possibility of speeding up and increasing our own program of biological control against the pest. The seriousness of the problem in the United States has, of course, increased tremendously now that the pest, or a very closely related one, has been found causing heavy mortality of Pacific silver fir (*A. amabilis* (Dougl.) Forbes) and subalpine fir (*A. lasiocarpa* (Hook.) Nutt) in Washington and Oregon.

In the Northeast the insect is limited to balsam fir; and it is now pretty generally distributed wherever this host occurs throughout the southern half of Maine, Vermont, New Hampshire, northwestern Massachusetts, and New York. It has not been found in the Lake States. It suffers severe winter mortality above the snow line when temperatures reach approximately  $-30^{\circ}\text{F.}$ , but is capable of building up rapidly when favored by mild winters. Severe tree mortality is now occurring in central Maine, southern Vermont, and locally in New Hampshire. Surveys have been conducted this summer to evaluate the damage caused by the pest on the Green Mountain and White Mountain National Forests.

Our latest estimate of the net volume of balsam fir on the Green Mountain National Forest was made in 1948. It amounted to approximately 50 thousand cords at that time. Mortality due to the aphid on the southern half of the forest has been high. In 1954 a  $2\frac{1}{2}$ -percent ground cruise was made on 300 acres in that section. The average merchantable volume of balsam fir was 11.06 cords per acre. Six percent of this volume had been killed by the aphid during the previous 5 years, and the total volume killed or infested was 44 percent.

This means that for every acre, .7 cord had been killed outright and 5.1 cords were either killed or infested. A re-check made this season indicates that losses have



increased to 21 percent of the volume killed and 75 percent of the volume killed and infested.<sup>1</sup> It has been decided to sell the pulpwood on the affected area, if possible before further losses occur. A cutting of some 2,500 cords is being made this season to determine whether or not an operation in the area will be profitable.

In central Vermont a survey was made on 400 acres in the Griffith Pond area east of Danby, 400 acres at Wallingford, and a 40-acre block near Rochester. In the Griffith Pond area the average volume of fir is 11.2 cords per acre. Eleven percent of this has been killed during the past 5 years and 53 percent is either dead or infested by the aphid. At Wallingford the area surveyed is largely spruce. There the survey showed about 5.5 cords of fir per acre; 25 percent of this has been killed. At Rochester 31 percent of the fir has been killed.

Our latest estimates of the net volume of balsam fir on the White Mountain National Forest were made in 1948 and 1953; they amounted to about 920,000 cords of growing stock. Generally speaking, young fully stocked stands are not infested at present. Surveys were conducted on 600 acres on Hancock Branch near Lincoln, N.H., and on 300 acres on Mill Brook near Stark, N.H. Data were averaged, and they gave the following results: volume of fir per acre, 12.0 cords; killed by aphid per acre, 1.0 cord or 8.5 percent; killed and infested by the aphid, 6.0 cords or 50 percent.

Losses on the areas surveyed are by no means representative of losses on the whole area of the Green and White Mountain National Forests nor on the forested areas of Vermont and New Hampshire. The surveys were made on susceptible areas known to be infested. Nevertheless, considering the total volume of fir on these National Forests, losses are very high — and considerably higher than anticipated. Unfortunately trunk attack is the prevalent type of infestation in Vermont and New Hampshire, and this type usually kills a tree within 2 or 3 years after the aphid starts to increase rapidly. However, a large proportion of the infested trees are still very lightly infested.

Estimates of damage in Maine have been kindly supplied by the Maine Forest Service. Trunk attack has wiped out much of the older fir in Washington and Hancock Counties. In recent years large quantities of fir have been killed from the Penobscot River between Orono and Mattawamkeag westward into western Maine. In many places the larger balsam has all been killed, unless cut. No definite figures on loss have been compiled; but in the area of attack the annual loss of merchantable fir is probably running 10 to 20 percent, and in many areas all merchantable fir is killed if it is not cut.

Along the coastal portion of the state, and to a lesser degree inland, the gout type of injury is most prevalent. This is most injurious on small young trees. Terminal growth is frequently stopped, and infested trees do not reach merchantable size. Therefore losses in volume are heavy. Probably 60 to 80 percent of the merchantable volume of fir has been lost in the affected areas.

In the Willamette Valley of Oregon, *C. piceae* has been attacking and killing grand fir (*A. grandis* Lind.) since about 1930. It has also been known to cause damage to subalpine fir. Until 1954 it had not been reported on Pacific silver fir growing under forest conditions. That year silver fir in Washington, especially on the Gifford Pinchot National Forest, was found to be seriously attacked by *C. piceae* or a very close relative; and observations indicated that the pest had been present for several years.

In 1955, epidemic infestations on Pacific silver fir were found to be more extensive and severe than in 1954. Measurable damage also occurred in Oregon on the Mt. Hood and Willamette National Forests. Surveys showed a total of 294,560 acres infested, 258,880 in Washington and 35,680 in Oregon. Of this total, 45,280 acres in Washington and 11,840 in Oregon were classified as heavily or very heavily infested. Severe mortality of large sawtimber-size trees has occurred in these areas. Plans for extensive salvage are being formulated and considerable salvage is already under way. On the eastern portion of the Mt. Hood National Forest considerable mortality of subalpine fir was also found in 1955.

The United States has done practically no biological-control work on the balsam woolly aphid; we have relied almost entirely upon the generosity and proximity of

<sup>1</sup>1954 data included all fir 1.6 inches and larger, while the 1956 data are based on merchantable trees 5.6 inches d.b.b. and larger.

our good neighbors. Both have stood us in good stead. The important predator, *Leucopis obscura* Hal., which was successfully introduced into New Brunswick in 1933, has spread naturally throughout the infested area of Maine; and last year colonies of both *Laricobius erichsonii* Rosenh. and *Pullus impexus* Muls. were made available for release in the United States. *Leucopis* may have spread naturally beyond the Maine - New Hampshire border, and it may have become established in southern New Hampshire from a colony received from Canada and liberated in Grantham in 1937. It seems unlikely, though, because a number of spot checks failed to disclose it; and the Grantham plot was cut soon after 1937.

Under the circumstances it was decided to undertake further colonizations. In cooperation with the Maine Forest Service, suitable collection areas were located in Maine in 1953 and five logs about 6 feet long, heavily infested with *Chermes*, were cut and overwintered at New Haven. About 500 *Leucopis* adults were recovered in the spring of 1954. They were colonized in southern Vermont, and establishment was confirmed this past spring. Similar *Leucopis* collections have been made in Maine for the past 2 years; and strong colonies have been liberated at two additional points in Vermont, one in New Hampshire and one in New York.

In 1955 both *L. erichsonii* and *P. impexus* were colonized in southern Vermont, and *Laricobius* was also colonized in New Hampshire. I am happy to report that *Laricobius* was recovered at the liberation point in southern Vermont this past spring. It is hoped that within a reasonably short time it will be possible to collect both these species for further colonization in the Northeast and perhaps the Pacific Northwest as well. In any event, the role these predators play in the current outbreak will be followed with special interest. Balsam is at the southern limits of its range in the Northeastern part of the United States, and this fact could be of considerable importance in the ecology of the *Chermes* predators.

In the Pacific Northwest, Mt. Hood area, two species of predators were found attacking the balsam woolly aphid: a new species of *Leucopis* and a *Pipiza* sp. Both species were collected from infested alpine fir. (They were abundant on only a few trees.) The effectiveness of these predators in controlling the aphid is yet to be determined.



# The Sugarcane Borers in Mexico. An Attempt to Control Them Through Parasites

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## ABSTRACT

The paper deals briefly with work accomplished during the last three years in the northwestern and northeastern coastal plains of Mexico, in order to seek possibilities of control of the sugarcane borers by means of their natural enemies.

*Diatraea considerata* Heinr., *D. grandiosella* Dyar and *Chilo loftini* Dyar in the northwest, and *D. saccharalis* (F.) and *D. magnifactella* Dyar in the northeast (all *Pyralidae-Crambinae*), are blamed for heavy losses and have been experimentally parasitized by *Diptera-Tachinidae* namely: *Paratheresia claripalpis* Wulp., *Palpozenillia palpalis* (Aldr.), *Lixophaga diatraeae* (Towns.), and in lesser amount *Metagonistylum minense* (Towns.).

Ecological conditions and the life-history of the borers, as well as the preliminary results are outlined. In general, work has not been as successful as expected due to the seasonal and daily variation of temperature and humidity, and specially the high temperatures of summer. While parasites can be reared only in the spring, the host population starts rising in summer. It seems that weekly mean temperatures of less than 20° C. or higher than 30° C. checks parasite development in the laboratory and reduces it considerably in the field; also, the established custom of burning cane before harvesting prevents continuity of parasitism.

## INTRODUCTION

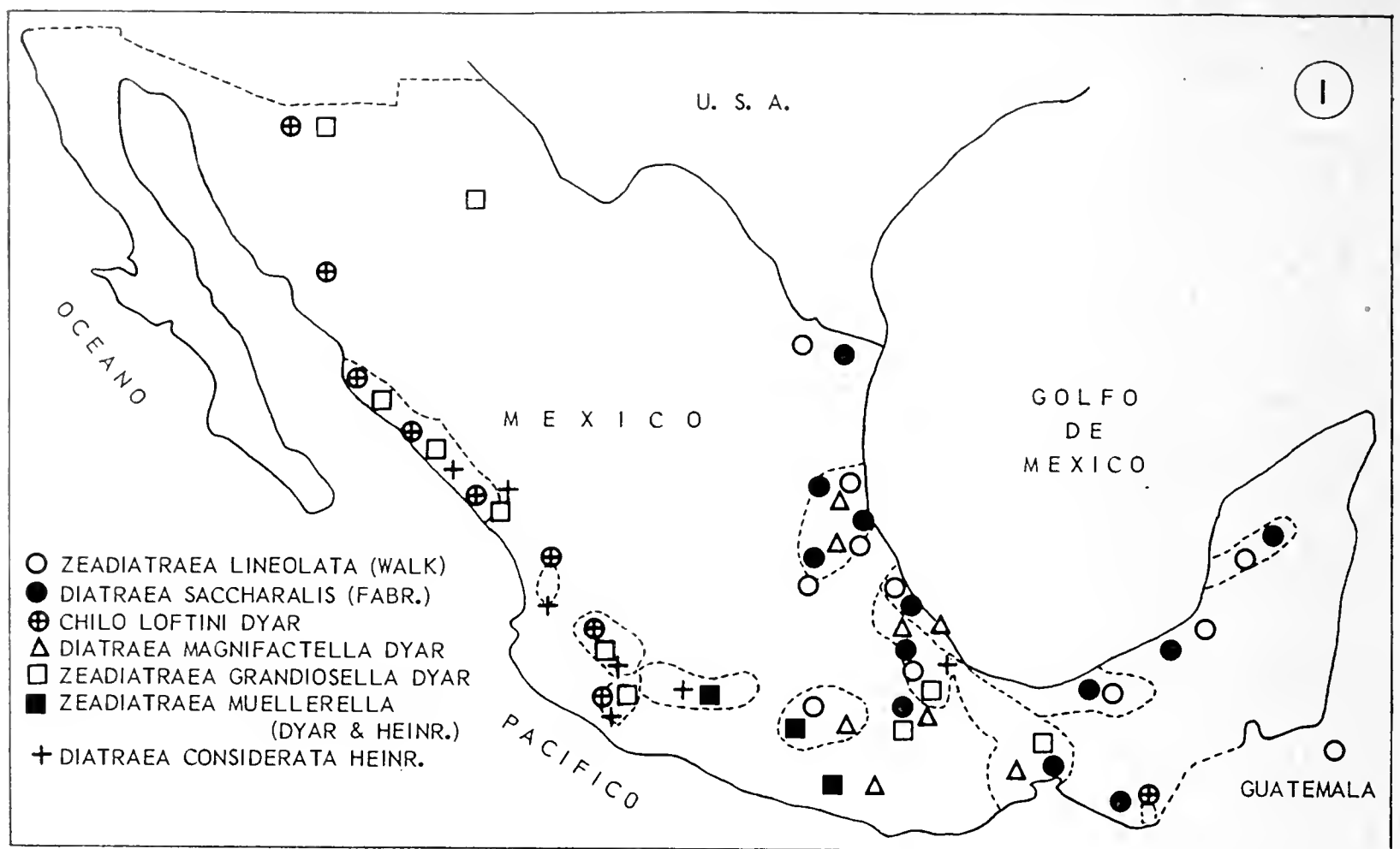
The moth borer (several species of *Pyralidae-Crambinae*) is the most important pest of sugarcane in Mexico. The character of the damage, fully described by several authors such as Holloway (1928), is accentuated in Los Mochis, La Primavera, Rosales, Eldorado and El Roble in the State of Sinaloa on the west coast, and in Xicoténcatl and El Mante on the east coast of Mexico.

Rojas (1953) established that in 1952 in El Mante, with an average infestation of 12.5 per cent, there were losses of more than \$2,500,000 Mexican.

This problem has been studied by several authors like van Zwaluwenburg (1926), who established the basis for later investigations. In 1947 he made a survey of the Mexican sugarcane pests and recommended trying to combat them with tachinid parasites. In 1950, Dr. L. C. Scaramuzza was invited to make a trip to the plantations and after gathering valuable data, he suggested contracting the services of Dr. H. E. Box. In 1950 and 1951, Box identified the species and outlined a preliminary program of control using especially the parasite *Paratheresia claripalpis* (Wulp) which is a native of Mexico. The recommended program has been conducted since the middle of 1951 and this paper deals with the work done to date (1956). (See Fig. 1).

According to Box the most common and injurious species that attack sugarcane are *Diatraea considerata* Heinr., *D. magnifactella* Dyar, *Zeadiatraea grandiosella* (Dyar), *D. saccharalis* (Fabr.) and *Chilo loftini* Dyar, although it is usual to find *Xubida dentilineatella* Bar. & McD. and other *Diatraea* sp. nov. in some parts of Veracruz. The most injurious to "maize" (*Zea mays* L.), are *Zeadiatraea lineolata* (Wlk.), *Z. grandiosella* (Dyar), *Z. muellerella* (Dyar & Heinr.); also, *Diatraea saccharalis* (F.) and *D. considerata* Heinr.

The tests were started in two places in 1951, Rosales plantation near Culiacán Sinaloa, and El Mante Tamps. where there were entomological laboratories and trained personnel.



## ECOLOGICAL NOTES UPON SINALOA AND TAMAULIPAS

### SINALOA

The State of Nayarit is located in the southwestern part of the Nearctic Region, approximately at the limit line of the Neotropical Region, while Sinaloa, can be considered as fully in the Neartic Region, precisely in a sub-region featured by its semidesertic regime.

Goldman (1951) identifies "provisionally" the coastal plains of the two states as arid lower tropical zones. The vegetation in Sinaloa is typically semidesertic; precipitation in the coastal plain (0 to 50 m. altitude) does not exceed 400 mm. (16") in normal years, while in central Nayarit (900 m. altitude), it is a little more than 500 mm. (20"). The rains in Sinaloa start in July and last until the middle of October, being followed by a long, dry season with occasional drizzles in January. The temperature is extreme, reaching in summer  $41^{\circ}$  C. in the shade and descending to the freezing point during winter. The relative humidity outside of the rainy season varies in accordance with the extension of the irrigated lands, since agriculture, especially the growing of sugarcane, is made possible by irrigation. Moreover, it has been noticed that the limiting factor for rearing and liberating parasites is the daily oscillation that very often reaches  $20^{\circ}$  C.

These comparisons between the plains of Sinaloa and the high valleys of Nayarit are made because of the fact that the infestation caused by the three species of the northwest, *D. considerata*, *Z. grandiosella* and *Ch. loftini*, never surpasses an average of 5 per cent in Nayarit, maybe because the weather favors the natural development of *P. claripalpis* and *Palpozenillia palpalis* (Aldr.) and almost 80 per cent of the fields are planted with the variety Co.290 that is less susceptible than POJ 2878, whereas in Sinaloa, the damages are desolating.

In Sinaloa due to the continuous clearing of lands for cultivation, the adult parasites lack shelter, specially in young cane and it is significant that the greatest number of *P. claripalpis* puparia for the laboratory breeding has been obtained from cane fields beside the rivers under the shade of trees.

### TAMAULIPAS

The only two plantations are located approximately at 100 km. from the littoral of the Gulf of Mexico and at less than 100 km. south of the Tropic of Cancer; it is considered as a marginal region for sugarcane cultivation and has a climate of a semidesertic type, dry and hot, without a definite winter season. The average annual



temperature is  $25.7^{\circ}\text{C}$ . with sudden changes and strong daily oscillations. The highest absolute temperature in summer is  $46^{\circ}\text{C}$ . and the lowest in winter is  $-4^{\circ}\text{C}$ . The total annual rainfall, June to October, is no more than 1,100 mm. (44") with a severe dry season of seven months. At the end of autumn and during winter there are strong winds from the north.

The natural semidesertic vegetation is very scarce and cultivation of sugarcane is done by irrigation, POJ 2878 being the dominant variety (80%) and the rest Co.290.

The dominant borer species are *D. magnifactella* and in lesser population (20%) *D. saccharalis*; *Z. lineolata* is specific on "maize" and along with *D. saccharalis* is parasitized by *P. claripalpis*. On the contrary, *magnifactella* is very seldom parasitized and its damages are like those of *considerata* in Sinaloa. It is believed that such species were introduced some years ago, probably through Córdoba, Ver., where hitherto they caused a small infestation of 5 percent.

## SOME DATA ON THE BORER BIOLOGY

### SINALOA

The winter determines real overwintering forms in *grandiosella*, and prepupae lose their spots and take a milky-white color from the end of October until April. Infestation in Los Mochis is notorious until the middle of June in the sugarcane tips and very seldom produces dead hearts. In 1926 Zwaluwenburg stated that in this region there are three generations of *grandiosella* per year, and that during the last months of summer it takes six to seven weeks for one generation. The above applies equally for the plantations of Culiacán, 200 km. south of Los Mochis.

The other two species, *D. considerata* and *Ch. loftini*, have a slight delay in their cycle during winter but remain active, specially Chilo, larvae of which have never been observed on the leaves, having preference for the stalk and buds and, therefore, decreasing the germination of sowing cane. Zwaluwenburg recorded 60 days for one generation during spring but Abarca Ruano observed that sometimes it takes up to 80 days. It can be found in all stages throughout the year, so the overlapping of generations is more complicated than in *Diatraea* and probably there are no less than six generations per year.

*D. considerata* is the most harmful; winter delays its cycle even up to 60 days but in spring and summer it averages 47 and is reduced to 37 in August, so there are more than five generations per year. The borer is larger than the others and in its course along the stalk, drills several internodes making real tunnels.

The maximum infestation of the three species, that is, the greatest number of young borers attacking the leaves and buds, starts in June (it coincides with the beginning of the largest growth of the cane), reaching its peak in August and September. Harvesting is done during winter and spring and the habit of burning cane before cutting prevents continuity of parasitism in case it could be attained. On the other hand the very young cane does not supply the necessary humidity to help the colonization at that time of the year.

### MANTE-XICOTÉNCATL

*D. magnifactella* is the dominant species in this region; *D. saccharalis* attacks with less intensity but they are found together without distinction in plants and ratoons.

The cycle of *D. magnifactella* is a little longer than that of *D. saccharalis*, with an average of 60 and 45 days respectively during summer and spring, lengthening during winter, without the appearance of overwintering forms. The insects can be found in all stages at any season; there is a continuous overlapping of generations and it has been estimated no less than eight generations per year.

## EXPERIMENTAL REARING AND RELEASE OF PARASITES

This was the first tried by Zwaluwenburg in Los Mochis more than 30 years ago. He imported and released *Lixophaga diatraeae* (Townsend) from the Antilles and *P. claripalpis* from Córdoba, Ver., without attaining colonization. In 1947, due to the study of pests patronized by Banco de México, S.A., he recommended the colonization

of *L. diatraeae* and *Metagonistylum minense* (Townsend). Thus, in June 1951, 2000 puparia of *Lixophaga* were imported from Trinidad and tested in El Mante, choosing fields with a prevailing population of *D. saccharalis*. Three months after the release, a cyclone did much harm to the plantations and when the survey was made the results of the colonization were nil. In June 1952, more than 2,000 adults were released but it was not possible to recover one single specimen of this lot.

In July 1951, 500 adults of *M. minense* (Amazonic strain) were released and in 1952, 100 San Paolo strain with negative answers. Simultaneous laboratory tests on *D. magnifactella* proved that these two tachinids are specific parasites of *D. saccharalis*, not being adaptable to *D. magnifactella* or to *D. considerata*.

The negative results of laboratory tests with these two parasites showed the impossibility of attaining control of the Mexican borer species with them and for this reason *P. claripalpis* was used. This insect of wide distribution, specially in maize, was recommended by Box in 1952, who suggested commercial breeding to produce no less than 50,000 flies per region yearly, trying to synchronize the releases with the season of greatest infestations that generally occur during spring and summer.

Based upon the location and the host it attacks, Box determined the existence of three strains of *Paratheresia*: PME strain, native of northern Veracruz, eastern San Luis Potosí and southern Tamaulipas, lives in cane and in maize attacking *Z. lineolata*, *D. saccharalis* and *D. magnifactella*; PMC, principally located in Córdoba, Ver., attacking *D. magnifactella* in cane and *Z. muellerella* in maize. It also exists in the states of Morelos, Guerrero and Puebla in the same species and hosts; PMW of Sinaloa and Nayarit attacking *D. considerada* in cane. Laboratory tests were made with these strains, using five species of borers, confirming that the PMC from Córdoba, Ver., and Chilpancingo, Gro., are the most promising against *D. magnifactella* and the PMW against *D. considerada*.

Finally, several crosses were made between PMW and PMC as well as between PMW and a strain from Perú. The results of these crosses were not superior to PMC.

#### RELEASING OF *P. CLARIPALPIS* IN SINALOA

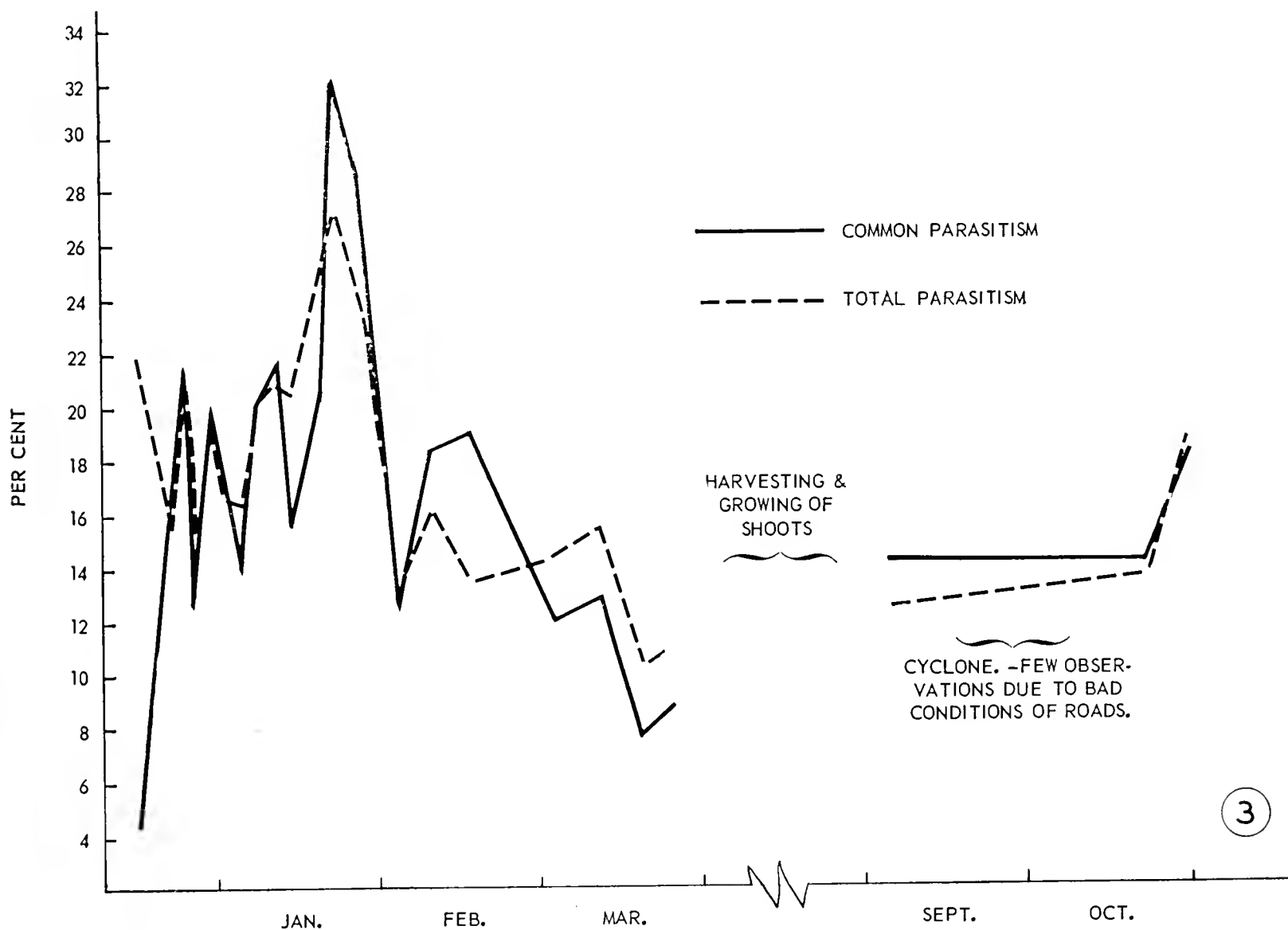
At the end of the spring of 1953 3,356 males and 3,542 mated females of PMW were released in Rosales plantation. During the autumn and the beginning of winter 152 couples of PMW were released, plus 43 males and 25 females of PP, and 427 borers artificially parasitized by PMW were introduced into the stalks by means of a hollow punch. Each strain or crossing was released separately at the rate of 15 couples per hectare every two weeks in fields with the greatest number of parasitizable borers (instars 4 and 5) near the irrigation canals. Most of the releases were made in young cane, but use was also made of a field which was not to be harvested that year and this was saturated with several strains and crosses.

During 1954, 4592 males, 4,305 females were released, as well as 700 borers previously parasitized with PMW. The annual survey showed a complete lack of colonization; after collecting more than 125,000 dead hearts from these fields only seven puparia were recovered. In the old canes, a 2 per cent parasitism was found in 1953, while in 1954, none was recovered.

While the yield of puparia was recorded in the laboratory, data on natural parasitism was taken at the field where the material was collected. Despite the presence of *Paratheresia* in this place, it had not spread to other lots, and infestation by the borer was never less than 25 per cent in 1953-54.

In Fig. 3 the common and total parasitism, with an average of 18 per cent, is registered from January to March but it decreases so that in June and July it is almost insignificant. It starts rising in September with a small decrease in November, and again reaches 18 per cent in January and February, when the cane is ready for harvesting.

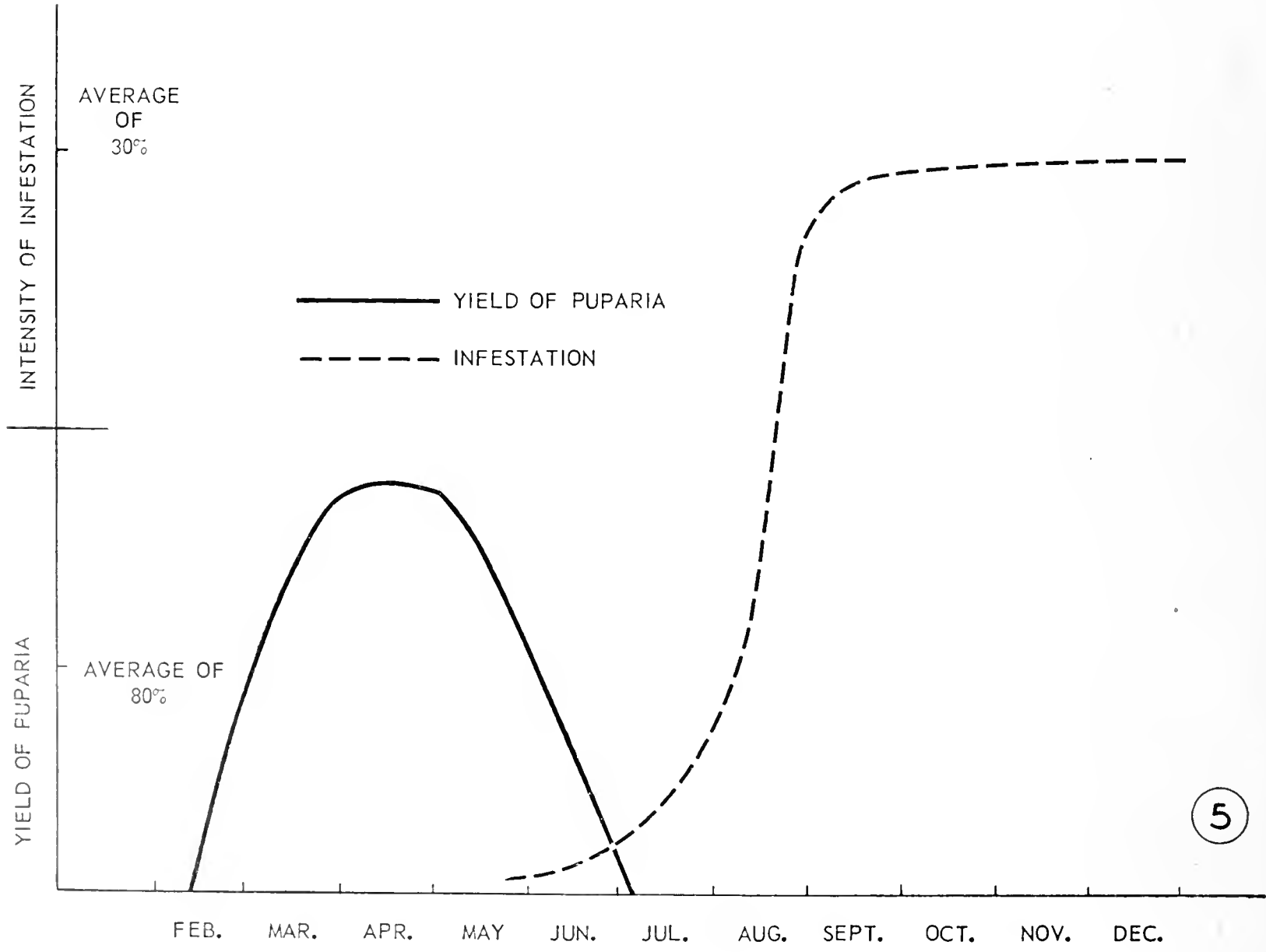
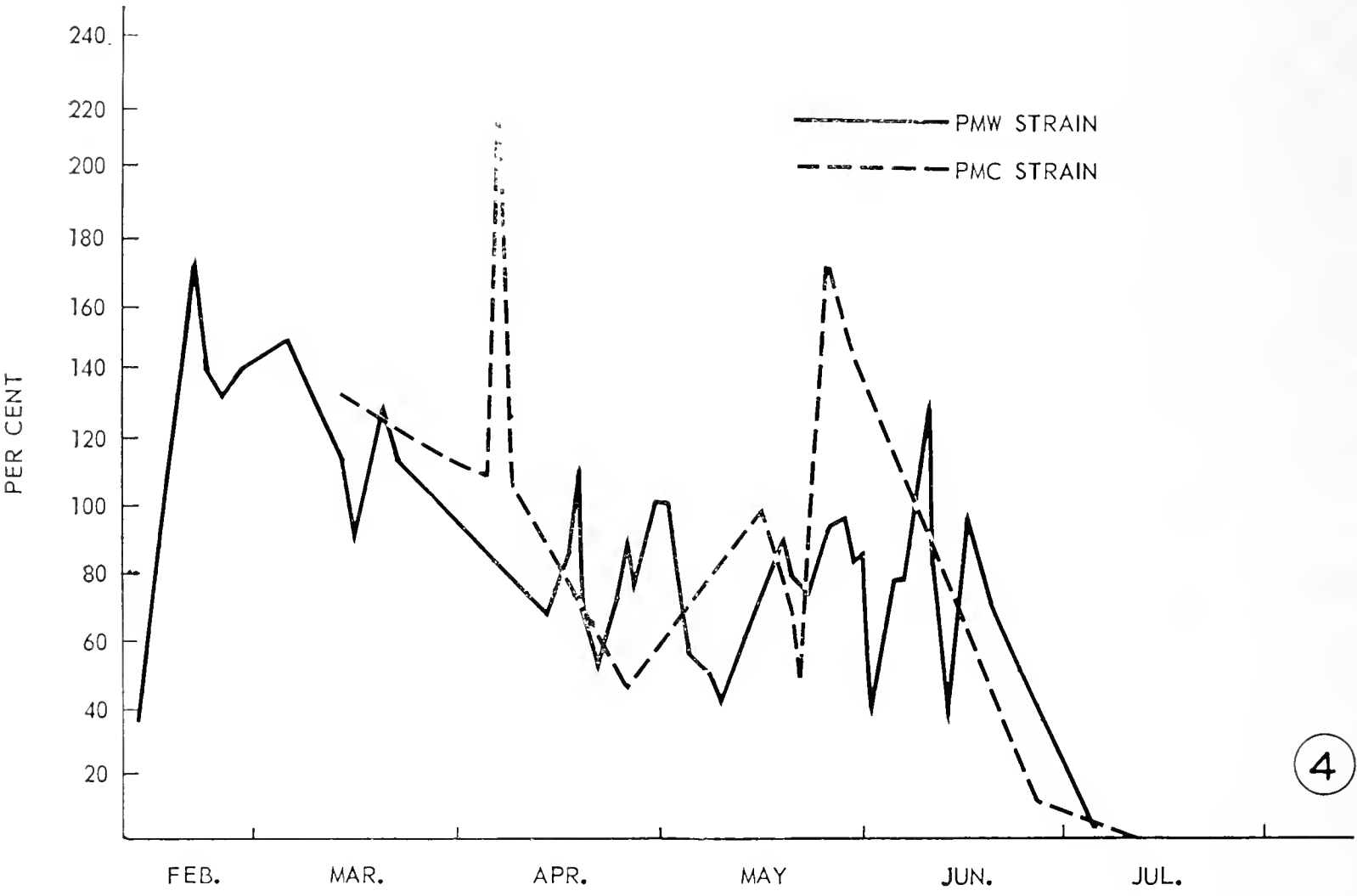
Artificial parasitism in the laboratory registered similar curves, as shown in Fig. 4, increasing in February, then dropping to 0 at the end of June or beginning of July. Before February the life of flies is longer than the time required for incubation of eggs (average of 12-14 days), but matings are rare and in case of incubation the number



of maggots per female is negligible. After June, life is much shorter than the time required for incubation and there are no copulations.

Good yields of puparia in the laboratory seem to be limited by the weekly average temperature of 20-30° C; the humidity has probably less influence, although rearing

does not thrive under a weekly average of 60, or over 90 per cent (see Fig. 2). There is another favorable period, that being at the beginning of autumn, but it cannot be used because of its briefness. Of all the tested strains and crosses against *D. considerata*, the graphical representation of the PMW native of Eldorado is the less irregular, probably due to its adaptability; it registers more copulations, longer life and more useful maggots.



## CONCLUSIONS OF THE REGION OF SINALOA

As can be seen, the seasonal abundance of host and parasite do not coincide, not because of lack of borers in the cane during January to June but on account of the cutting of the cane. Later, the new cycle of infestation starts intensely in June, free of parasites because they cannot multiply during summer. Moreover, the microclimate of young cane during spring does not favor the development of the parasite. Fig. 5 is a comparison between yield of puparia in the laboratory propagation and rise of borer infestation in the field. It might seem an aberration since it compares the population of parasites with the harm of borers, but it is only shown as an illustration. Note that the only connection point between curves occurs during June. The ideal would be a wider area of connection.

Besides the above-mentioned, other preliminary conclusions are:—

- (1) Biological control with these parasites is very difficult to attain in continental regions where the climate is extreme and especially if it is arid.
- (2) Up to date (1956) only *D. considerata* has been susceptible to parasitism, and *Z. grandiosella* and *Ch. loftini*, that produces 48 per cent of the total damage, are not attacked by *Paratheresia*.
- (3) The parasites are highly susceptible to insecticides which are applied in Culiacán, Sin., each year in great quantities to the cotton culture.
- (4) The cost of the released flies is exceedingly high and with little probabilities of success.

RELEASES OF *P. CLARIPALPIS* IN EL MANTE

During 1954-55 there were released in several fields near the canals 9,429 *Paratheresia*, half males and half females, previously mated and in quantities greater than 20 insects per hectare, several releases being made in each field with intervals of from three to four weeks. The survey made three months after the last release showed very little parasitism of *D. magnifactella* and from *D. saccharalis* recovering in five tested fields 578 living puparia.

In this region the problems are similar to those of Sinaloa with regard to temperature and relative humidity. The critical months for the laboratory breeding include from May to the end of August, when the temperature rises over 40°C. There are also many cloudy days, that check matings of *Paratheresia* in the laboratory, and the abrupt changes in temperature and the winter winds cause great mortality among flies. Nevertheless, in this region the conditions seem a little more favorable to attain the biological control of *D. magnifactella*.

Of the above-mentioned *Paratheresia* strains the PMC of Córdoba, Ver., and Iguala, Gro., proved to be adaptable to *D. magnifactella* in the laboratory, as well as in the fields.

There is still much uncertainty concerning the value of this work due to the fact that it has not been possible to organize the commercial breeding to provide for the release of 50,000 flies per year at each of the two places. However, the total number of parasites released during the last three years (no less than 25,000) and the preliminary data gathered, indicate that *Paratheresia* could continue to give negative results.

The preliminary results make it evident that it may be convenient to keep experimenting with *Paratheresia* at El Mante and discontinue it in Sinaloa. To solve this problem Box recommended experimenting also with *Palpozenillia palpalis* (Aldr.), which exists naturally in several parts of the country. It is also necessary to make a parasite search in other countries for introduction and experimentation against the Mexican *Diatraea* giving special attention to those insects that parasitize larvae of Pyralidae-Crambinae on wild and cultivated gramineous plants.

As a new approach, a laboratory has been established in Iguala, Gro., where *Z. muellerella* in maize is heavily attacked by *Palpozenillia* and *Paratheresia*. From here puparia will be shipped to the places where they are necessary and at the time they are needed. The problems yet to be solved are rearing during the summer and development of techniques for reproduction of *P. palpalis* that is oviparous.



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# Biological Control of the Oriental Fruit Fly in Hawaii

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## ABSTRACT

On reaching Hawaii (probably in 1945), the oriental fruit fly, *Dacus dorsalis* Hendel, increased rapidly into an extremely serious pest and the Board of Agriculture and Forestry promptly sent explorers to the Orient in search of parasites of this tephritid fruit fly. Due to the damage done and the menace to the mainland United States created by its presence in Hawaii, funds were allocated by a number of agencies for a large scale cooperative program which resulted in additional explorers being sent to many parts of the world to make a thorough search for parasites. Subsequently, some two dozen species of parasites were shipped to Hawaii for release but only three of these played a significant role in bringing the pest under control. Furthermore, only one of these parasites, *Opius oophilus*, Fullaway, is important today. It became established in 1949, rapidly became the dominant parasite and since 1952 has been the only parasite of importance. Establishment, spread, build-up, and status of both host and parasites have been followed at monthly intervals for the past six to seven years, and during the last five years parasitization by *O. oophilus* has been around 70 per cent, as determined by rearing. However, tremendous numbers of the parasitized eggs are killed prior to hatching due to infection by microorganisms inserted at the time of oviposition. In fact, mortality due to parasitization by this species normally exceeds 95 per cent. The population of and damage by the fly today is no more than 5 per cent of what they were at the peak abundance of the pest in 1948-49. Trap catches, infestation indices, and parasitization at monthly intervals are shown graphically for 1950, 1952, and 1955 and summarized in tabular form by years for the period 1950-55.

The oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae), was first found in Hawaii in 1946 and within a year reached epidemic populations throughout the Territory. Damage was so severe that public concern was aroused both in Hawaii and on the mainland United States. In the spring and summer of 1948 entomologists of the Territorial Board of Agriculture and Forestry introduced three species of parasites reared from *D. dorsalis* in Malaya which subsequently proved important in the biological control of this fly in Hawaii. In the same year several agencies (Carter, 1950) joined together in a cooperative control program and during the next several months had explorers searching for parasites and predators of fruit flies in many different countries. A detailed study has been made of the progress of the introduced parasites and the status of *D. dorsalis* throughout the past seven years to evaluate the effectiveness of the biological control program. This discussion will be confined to the high points of this phase of the study.

## METHODS

During the first several months of the study in the fall of 1948 and 1949 when *D. dorsalis* was extremely abundant, infested fruits of many species were collected to determine the progress of the parasites; however, late in 1949 it was decided to restrict the regular collections to guava, *Psidium guajava* L., since it grows wild over large acreages, fruits throughout the year, and is the principal host of the fly in Hawaii. In 1949, 40 collecting sites were established on Oahu where guava fruits were collected each month. During the first three years or so, 20 or more fruits were collected at each site, but later it was decided to reduce the number of fruits collected to 4 and to increase the number of collecting sites to 60. The fruits were carefully dissected in the insectary, and the number of maggots in each fruit recorded. The maggots were then transferred to a blended papaya medium and held until the adult flies and parasites emerged. In addition, collections of guavas have also been made two to three times a year on the outer islands, and fruits other than guava have been collected from time to time throughout the period of study.

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To obtain a general estimate of fly abundance, specially designed traps (Newell and Haramoto, in press) using methyl eugenol, a male lure, have been operated continuously for the past six years at 11 different sites in guava areas on Oahu. The traps were serviced monthly and the catches measured volumetrically (1 cc. = approximately 24 flies).

### PROGRESS AND STATUS OF *D. DORSALIS* AND ITS PARASITES

*D. dorsalis* became extremely abundant shortly after it reached Hawaii and remained so throughout 1947, 1948, and 1949. Indices of the fly population and fruit infestation were many times greater than when the regular systematic studies were begun in 1950. At that time most tree fruits were so heavily attacked that they either dropped prematurely, were malformed, or contained many maggots and were unfit for human consumption. The fly was reared from over 100 different kinds of fruits, and such fruits as mangos, avocados, and guavas commonly contained more than 100 larvae per fruit. These fruits could only be used when they were protected by bagging.

Following the introduction of parasites during 1948 and their rapid increase, there was a sharp decline in the fly population and infestation of all fruits in 1950. A still further decline occurred in 1951 (Figs. 1, 2), and since then the population and infestation have been relatively stable (Table I). During this five-year period, the fly catches have averaged about one-fourth and the infestation, based on larvae per guava fruit, about one-half of that in 1950. Nevertheless, in 1955, 60.5 per cent of the guavas in the samples were attacked as evidenced by ovipositional punctures; however, only 22.2 per cent contained maggots. Fruits like avocados, bananas, lychees, and papayas, which were once heavily attacked, are now seldom attacked. The damage to mangos is somewhat higher, but infestation seldom exceeds 10 per cent even without spraying. Within recent years many vineyards of passion fruit have been established at lower elevations in agricultural areas where *D. dorsalis* and *D. cucurbitae* Coquillett occur together and oviposit in this fruit. In most instances the larvae do not develop, therefore, the damage attributable to *D. dorsalis* cannot be readily determined. However, the combined attack by both species is seldom high enough to warrant spraying of the vineyards.

Between 1948 and 1952, one predator and 31 species of parasites of fruit flies were introduced; however, only the three Malayan species, *Opius longicaudatus* (Ashmead), *O. vandenboschi* Fullaway, and *O. oophilus* Fullaway, were important in the reduction of *D. dorsalis* during 1948 to 1950. After *O. oophilus* assumed predominance in 1950 the other two species virtually disappeared on Oahu during that year and on the other islands during the following year (Bess, et al., in press). *O. longicaudatus*, which attacks mainly second- and third-instar maggots, was the first to become established, and during the spring and summer of 1949 an average of about 15 per cent of the maggots in the guava fruit samples were parasitized. However, parasitization exceeded 50 per cent in certain localities. *O. vandenboschi*, which attacks first-instar maggots, assumed predominance over *O. longicaudatus* in September of 1949 and for the following 12 months parasitized about 30 per cent of the maggots. *O. oophilus*, an egg-larval parasite, was first recovered in December 1949, but by the following July it had become the predominant parasite. Since that time parasitization by this species based on rearings of larvae from field-collected fruits has averaged about 70 per cent. Actually, a much higher percentage of the population is destroyed, for it has been found that many of the eggs attacked are killed by fungi and bacteria introduced at the time of oviposition by *O. oophilus* (Newell and Haramoto, in press). For example, out of 1579 eggs examined from guavas collected in 1955 and held in the insectary two days for hatching prior to examination, 513 eggs hatched and 1066 eggs failed to hatch. One thousand and two eggs of the latter group were parasitized but failed to hatch due to infection by microorganisms. Three hundred and sixty-eight *O. oophilus* adults and 103 flies emerged from the puparia that were formed from the maggots of the hatched eggs, representing a parasitization of 78.1 per cent; however, 73.1 per cent of the parasitized eggs had failed to hatch due to infection by microorganisms. Therefore, actually 86.8 per cent of the eggs in these fruits were parasitized. Although egg parasitization by *O. oophilus* usually exceeded 90 per cent, this example

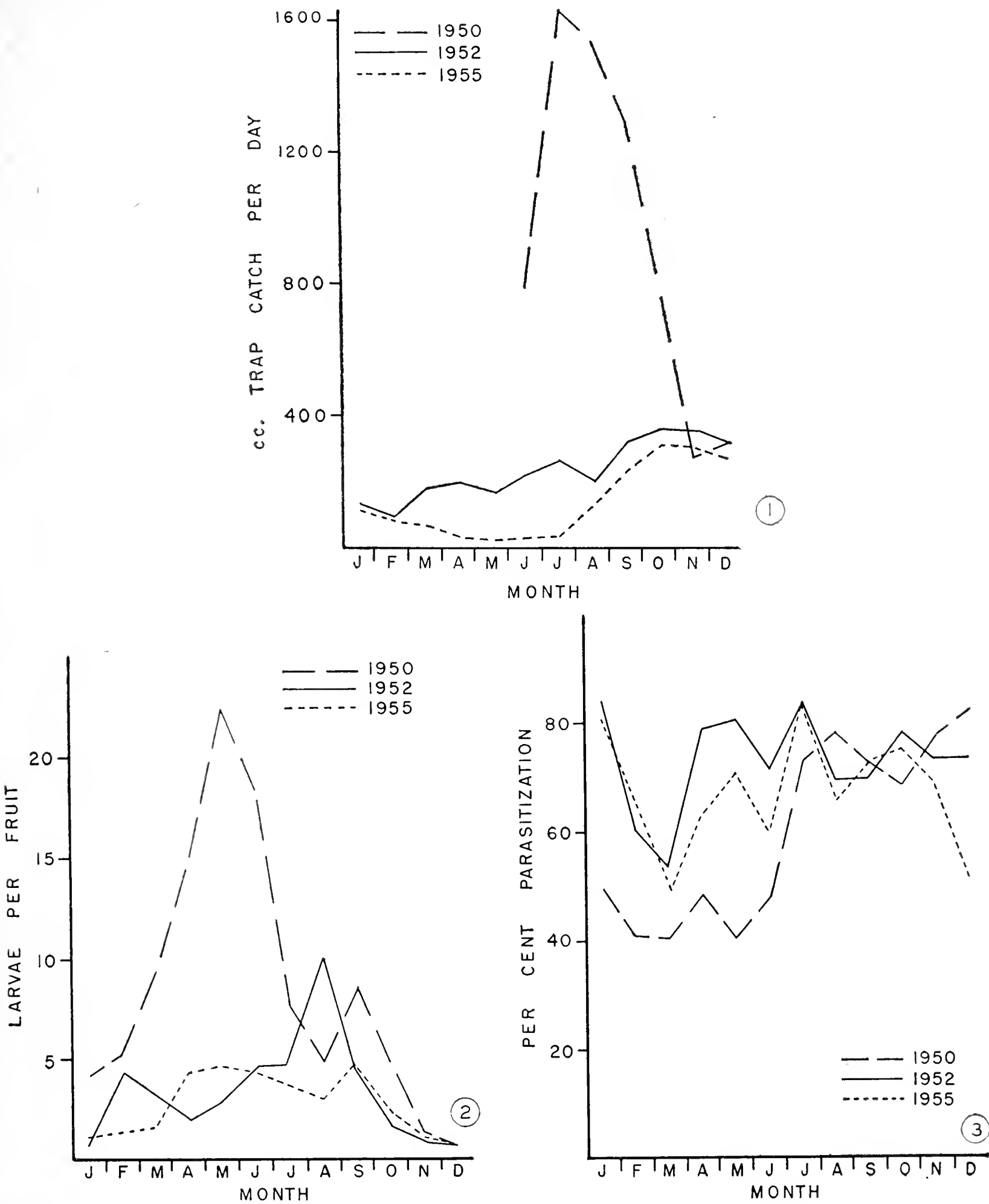


Fig. 1. Graph showing *D. dorsalis* males caught monthly per day per 11 traps on Oahu during 1950, 1952, and 1955.  
Fig. 2 Graph showing larvae per fruit in guavas collected monthly from permanent sites on Oahu during 1950, 1952, and 1955.  
Fig. 3. Graph showing monthly parasitization of *D. dorsalis* maggots in guavas collected from permanent sites on Oahu during 1950, 1952, and 1955.

TABLE I — Yearly Averages of Trap Catches, Fruit Infestation and Parasitization Obtained from Permanent Collection Sites on Oahu from 1950 to 1955.

	1950	1951	1952	1953	1954	1955
Cc. of <i>D. dorsalis</i> males caught per day per 11 traps	940	227	232	245	220	145
Larvae per guava fruit	8.5	2.6	3.3	6.9	4.3	2.6
Per cent parasitization*	60.0	79.1	72.1	70.3	71.7	67.1

\*Based on rearings of larvae from field collected guava fruits.

illustrates the high mortality of parasitized eggs caused by microorganisms. Practically all parasites reared from *D. dorsalis* during the past four years have been *O. oophilus*. Parasitization based on rearings of larvae alone each year for the past five years has been between 79 per cent in 1951 and 67 per cent in 1955, or an average of 72 per cent (Table I). The monthly average parasitization during this period varied between a high of 91.7 per cent in December 1951 and 48.2 per cent in March 1955 (Fig. 3).

### GENERAL DISCUSSION

The large quantities of host fruits throughout the year in Hawaii, especially guavas, were a big factor contributing to the rapid build-up of *D. dorsalis* immediately following its introduction. The flies produced in these guava areas move about freely and attack cultivated fruits, such as mangos and passion fruits. Billions of flies were produced during 1947 and 1948; and as late as July 1950, after there had been already a great reduction in the population, the traps caught an average of 85.5 cc. or approximately 2000 male flies per trap per day from June through December. Once the parasites gained a firm foothold in 1949 and 1950, the fly populations rapidly declined, and during the same period, June through December 1951, the catch averaged 20.6 cc., or approximately 500 male flies per trap per day. The average for these months, which is the period when the catches are highest, has been about the same each year since 1951, the average in 1955 being 18.2 cc., or approximately 450 male flies per trap per day. There was also a great reduction in fruit infestation, and many kinds of fruits that were once heavily infested have been practically free from attack during the past five years. Furthermore, *D. dorsalis* is no longer a pest at higher elevations where it was once a serious pest of crops such as peaches, loquats, and persimmons. Apparently the injury to these fruits during the peak years of *D. dorsalis* was due to the overflow of flies from the vast populations produced at that time in fruits at lower elevations. The trap catches and fruit infestation have been consistently higher in certain localities than in others; nevertheless, they have been much lower in all localities than prior to 1950.

In the summer and fall of 1948, when the first releases of the Malayan parasites were made, *D. dorsalis* was extremely abundant everywhere; therefore, the parasites had a good opportunity to become established, build up quickly, and spread rapidly throughout the islands. All three of these parasites of *D. dorsalis* in Malaya not only became promptly established and increased but also at the height of the abundance of them literally thousands of adults, predominantly males, could be seen hovering over or resting on low vegetation in protected sites in partial shade within guava areas. Since *O. longicaudatus* was easier to mass-breed in the insectary, this species was released in greater numbers, even though far fewer were received in the shipments from Malaya than the other two species, *O. vandenboschi* and *O. oophilus*, referred to at the time as one species under the name *O. persulcatus* (Silvestri) (Bess, van den Bosch, and Haramoto, 1950). This in part accounts for the establishment of *O. longicaudatus* prior to that of the other species and its abundance during 1949. However, by the fall of 1949, *O. vandenboschi* had increased to tremendous numbers and became far more abundant than *O. longicaudatus* on Oahu, parasitizing about 30 per cent of *D. dorsalis* maggots in guavas, as compared to a parasitization of about 10 per cent by the latter parasite. *O. vandenboschi* continued to be abundant, parasitizing about 30 per cent of the maggots until the following summer when *O. oophilus* became the predominant parasite. Since December 1950, *O. oophilus* has continued to parasitize upwards of 70 per cent of the population based on rearings of larvae, and both of the other parasites have become extremely scarce. Actually the parasitization of *O. oophilus* has been considerably higher than these figures indicate because of the high mortality of attacked eggs due to infection by microorganisms. Despite the high mortality of *O. oophilus* due to microorganisms, this parasite continues to parasitize an exceedingly high percentage of the *D. dorsalis* population, which now is much lower than it was shortly after it became established.

Factors contributing to the predominance of *O. oophilus* during the past five years and the concurrent reduction of *O. longicaudatus* and *O. vandenboschi* are worthy of



discussion. During 1955, only three specimens of *O. longicaudatus* and none of *O. vandenboschi* were reared from the regular guava fruit collections. The stage attacked is important from the standpoint of competition among species. *O. oophilus* oviposits in eggs which are laid massed together in a pocket just beneath the fruit surface; *O. vandenboschi* oviposits in young small maggots which are still fairly well grouped in and near the oviposition pockets; while *O. longicaudatus* oviposits in larger, more active maggots which become scattered in the fruit as they develop and are usually some distance from the rind. Therefore, the later the stage attacked the greater the difficulty involved in oviposition. Furthermore, van den Bosch and Haramoto (1951) found that *O. longicaudatus* larvae could not develop in maggots that contained larvae of either *O. vandenboschi* or *O. oophilus* larvae, and *O. vandenboschi* eggs are inhibited from hatching in maggots that contain *O. oophilus* larvae. Therefore, if *O. oophilus* had become abundant before the other parasites, probably neither *O. longicaudatus* nor *O. vandenboschi* would have played a role of importance in the control of *D. dorsalis* in Hawaii. Even though these two opiines are scarce today, during their peak abundance they destroyed millions of *D. dorsalis* and therefore reduced the injury that would have occurred in 1949 and 1950 prior to *O. oophilus* taking over.

It was fortunate that these systematic ecological studies were begun while the fly was extremely abundant and causing widespread destruction to fruits and that they could be continued over several seasons after the parasite introductions so that the effectiveness of the biological control program could be assessed. Between 1947 and 1949, before the parasites began to take a heavy toll of *D. dorsalis*, the infestation was tremendous with practically 100 per cent of most kinds of fruits infested. At that time, *D. dorsalis* was a serious pest from sea level to 5000 feet elevation. With the establishment and buildup of the three Malayan *D. dorsalis* parasites, the infestation rapidly declined. Since 1951 cultivated fruits such as loquats, peaches, and persimmons grown at elevations above 2000 feet and avocados, papayas, and bananas grown at lower elevations have been essentially free from attack. Furthermore, mangos have seldom been attacked to the extent of 10 per cent of the fruits even without the application of insecticides or mechanical control measures. Nevertheless, the infestation in guavas, which produce the bulk of the *D. dorsalis* populations in Hawaii, is still sufficiently high to cause concern because of the greatly expanded uses made of guavas recently. In addition, it may be of interest to point out that the occurrence of *D. dorsalis* in Hawaii prevents the movement of host fruits to export markets without fumigation or other satisfactory treatment.

The great reduction in the population of and damage by *D. dorsalis* was due largely to the activities of the introduced parasites. It has been found that during the past five years upwards of 90 per cent of *D. dorsalis* progeny were attacked and destroyed by *O. oophilus* and that very little mortality was caused by other factors. Without doubt, this parasite has been the principal factor in reducing the abundance of and damage by this fly and has continued to be effective in holding the fly in check through several generations during the past five years.

### SUMMARY

The population density of *Dacus dorsalis* Hendel from its discovery in Hawaii in 1946 through 1955 is discussed. The population reached its peak heights between 1947 and 1949, declined sharply during 1950, and has remained stable at a much lower level for the past five years.

Prior to 1950 the numerous flies produced in the large guava areas moved about freely, inflicting serious damage to various kinds of fruits; but once this large reservoir of flies had been reduced, many of them have been practically free from attack. Correlated with the sharp drop in the fly population density was an increase in parasitization. Several species of entomophagous insects were introduced to combat fruit flies in Hawaii, but only three of them, *Ophius longicaudatus* (Ashmead), *O. vandenboschi* Fullaway, and *O. oophilus* Fullaway, were important in the reduction of the *D. dorsalis* population. The progress, status and role played by each in the control of the fly are discussed. The first two species became scarce by the end of 1950 after *O. oophilus* had become the predominant parasite in July and increased tremendously during the fall.

Since that time *O. oophilus* has been the only species of importance in the further reduction of the fly population density and in keeping it in check at the reduced level. Despite the heavy losses suffered by this parasite due to high mortality of parasitized host eggs by microorganisms, parasitization as determined from monthly rearings of larvae in field-collected fruits has been about 70 per cent throughout the past five years.

The information obtained from the systematic monthly guava and trap collections over the past six years gives strong evidence that biological control was successful.

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# The Retardation of the Japanese Beetle, *Popillia japonica* Newman<sup>1</sup>

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## ABSTRACT

*With the invasion of Maryland by the Japanese beetle a retardation program was set up. Every known method of control was used by official agencies and the public. These methods consisted of trapping, spraying, selective planting of trees and shrubs, changes in the dates of planting the principal crops such as corn, and the use of parasites and the so-called "milky" disease. There have been distributed 1178 colonies of parasites and over 160,000 pounds of spore dust inoculum plus approximately 26,000 packages of contaminated soil on over 123,000 properties or colony sites. The effectiveness of insect parasites, predators and disease is such that there should be no great general infestations in the future.*

The Japanese beetle was first discovered in Maryland in 1927. The history of the insect in other states indicated that the best degree of control in Maryland that could reasonably be expected would constitute merely a retardation. Hence with this philosophy in mind the total efforts of officials and non-officials in Maryland were directed toward reduction of the number of the beetles by every know feasible method: trapping, soil poisoning, spraying foliage with repellents and poisons, the utilization of several agronomic practices, selective planting, and biological control were used to the best advantage possible.

Traps and attractants were improved materially and were used on a lease basis by most of the farmers and many urban dwellers. Thus besides actual destruction of millions of beetles, we had a complete index of population throughout the invasion of the state. This index enabled us to measure the reduction of beetles as affected by all of the retardation methods.

Traps at the height of the infestation caught over 369 tons of beetles in a single season. Automatic killing of beetles that are attracted to traps is possible, but no record of the total catch is available from such traps. The public generally seems to prefer the traps that retain the beetles so that they can measure or estimate the catch.

Soil poisoning against the grubs with arsenate of lead at the rate of 450 lbs. per acre was effective in preventing injury to turf in the early stages. After the advent of DDT that material at 25 lbs. per acre proved equally effective and was generally substituted for arsenate of lead in this part of the program. General treatment of nursery rows and treatment of sod on urban and suburban properties, together with a small amount of farm turf treatment undoubtedly exerted some influence on the success of the retardation program.

There was quite general spraying of apples and peaches with arsenate of lead and lime. The repellency was more marked than the killing of beetles. Likewise, elm trees were quite generally sprayed with arsenate of lead and lime in the early stages of the program. Many dead beetles were seen on the ground under sprayed trees, but the foliage was only partially protected from the feeding damage.

When DDT became available the public generally began spraying trees, shrubs, farm crops and orchards with resulting heavy destruction of beetles. In addition, a program of roadside and farm crop treatment on a demonstrational basis was inaugurated in cooperation with the county governments.

Mist blower applications of DDT and BHC in concentrated forms were made in 1948 and 1949 along all of the state and county roads in three counties. These treatments resulted in the destruction of thousands of beetles, as evidenced by the continuous windrows of dead beetles along the road edges and decrease in foliage damage along the fence rows. During the same years due to the extensive infestation of the European corn borer in the same counties many demonstrations of mist blowing of concentrated

<sup>1</sup>Miscellaneous Publication No. 274, Contribution No. 2739 of the Maryland Agricultural Experiment Station, Department of Entomology.

sprays on corn were conducted. Farmers had been encouraged to plant a trap crop of soybeans around the corn and early application of these trap crop rows further reduced the beetle population.

Mid-season planting of hybrid corn so as to avoid the conjunction of beetle peak and corn silking, the planting of soybean trap crops, and weed destruction by chemicals were some of the agronomic practices that tended to retard the multiplication of the beetles.

The attempt to induce land owners to use selective planting was not very successful. Despite the circulation of lists of favored food plants, newspaper and radio coverage and constant reference to the subject before garden clubs and farmer meetings, land owners continued to plant such susceptible trees as the American elm, pin oak and flowering crab apple.

The really successful use of biological control was the outstanding feature of this campaign of retardation.

Two parasites imported by the United States Department of Agriculture have been used. The first introduction was of two colonies of *Tiphia vernalis* Rohwer liberated at Colgate in Baltimore County and at Elkton in Cecil County in 1934. Later in the year 2 colonies of *Tiphia popilliavora* Rohwer were liberated in the same areas.

An attempt was made to rear *Tiphia* parasites in tin salve boxes, but after one season of experimental work it seemed much more economical to pay men to collect the parasites in New Jersey and Pennsylvania where they had been established for a number of years. This process of collecting in other states and liberating the colonies in Maryland was continued for several years until the original releases in Maryland had become thoroughly established and colonies could be collected for redistribution. With the original colonies, those collected in other states and those collected in Maryland, 1178 colonies of 100 females have been liberated. These digger wasps are established in all of central Maryland, in some parts of western Maryland and on the eastern shore of the state.

The most important retardation effort was the thorough dissemination of two bacterial diseases of the grub of the Japanese beetle. The milky diseases are caused by either one of two spore-forming bacteria known as *Bacillus popilliae* Dutky and *Bacillus lentimorbus* Dutky. The former is the predominant species and is responsible for what is known as Type A disease. The latter causes what is known as Type B disease. The milky disease organisms are spore-forming bacteria that live principally in the blood stream of the grub, although they may occur in the pupa and adult. They are exceedingly effective in destroying Japanese beetle grubs, but for quick and effective establishment they must have a heavy concentration of grubs in the soil. Once all of the land in a community is thoroughly inoculated with milky disease organisms it is not possible for large numbers of grubs to survive and produce beetles. The efficiency of the disease may be attested by results obtained at the Prince George's Country Club. In 1940 the grub population of the fairways ranged from 20 to 60 per square foot. Treatment of the golf course reduced the grub count to from 1 to 3 per square foot. This low infestation has been maintained without additional treatment for a period of nine years.

Disease establishment work has been a major activity in the Maryland Japanese beetle retardation program. It has gone forward at a rapid pace, and its value is reflected in the fact that where disease has been thoroughly established Japanese beetle damage has been greatly reduced. Between October 1, 1939 and September 30, 1954, 160,490 pounds of milky disease spore dust and 26,449 packages of disease inoculated soil have been prepared from grubs inoculated in the Maryland laboratory. This spore dust and inoculated soil has been distributed on 123,298 colony sites.

The original scheme for the distribution of milky disease in the heavily infested areas was treatment of soil on the basis of 3 one-acre plots in each square mile, for rural areas. In cities and towns treatments were made on one or more properties in each city block. When this distribution was completed in any county, intervening acres and more homes in city blocks were gradually treated in an effort to achieve complete coverage. The manufacture and distribution is being continued and the redistribution

of parasites will be continued. At the present time the grubs of the Japanese beetle are so scarce or so scattered in their distribution that the supply is inadequate in Maryland. This contrasts strongly with the abundance in early times. For the past four years grubs have been brought in from Virginia where individuals dig and sell them to us for processing.

The production of milky disease spore dust is somewhat costly and rather slow because of the technique required. The process of culturing the organism is as follows: Each day, laboratory technicians seated before microscopes inject into each grub with hypodermic needles a bacterial solution containing about 2,000,000 spores. After injection, each grub is placed in a separate cell in a box with a capacity of 500 Japanese beetle grubs, which in turn is taken to an incubating room where a constant temperature of 85°F. and 85 per cent humidity is maintained. For the next ten or twelve days the grubs feed on germinating clover and red top seed mixed in the soil of their compartments. At the same time the disease develops to a point where each grub contains from two to five billion bacterial spores. At the end of this period the sick grubs are removed from the incubating room, ground to a pulp, and then mixed with chalk and talc so that a standardized material is obtained which can be used in establishing the disease on grub-infested land, at the rate of 2 pounds per acre.





# Achievements in the Biological Control of the Sugar Cane Borers *Diatraea* spp. (Lepidoptera: Pyralidae) in the Americas

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## ABSTRACT

The most important pests attacking sugar cane in the Americas are borer larvae of several species of moths belonging to the genus *Diatraea*. At least 16 species have been recognized but the well-known species, *D. saccharalis*, is responsible for the greatest damage. Due to their habit of burrowing in the canes, control by insecticides is costly and of questionable value. On the other hand, the use of natural enemies has given practical control in all countries where full advantage has been taken of its possibilities. About 30 species of larval parasites are known but of these only three species have been used extensively, namely, *Lixophaga diatraeae* Towns., *Metagonistylum minense* Towns. and *Paratheresia claripalpis* v.d.W. The value of artificial multiplication and release of native parasites has been well known by the results obtained with *Lixophaga* in Cuba and *Paratheresia* in Perú, both being indigenous parasites of these countries. *M. minense*, obtained from borers in native grasses on the banks of the lower Amazon River, was remarkably successful in several countries.

It is a well known fact, that the most important pests attacking sugar cane in the Americas, are the small borer larvae of different species of moths belonging to the genus *Diatraea*. Their ravages are causing a loss conservatively estimated at not less than \$60,000,000 annually.

Although there are not less than 16 species of *Diatraea* which attack sugar cane in the Americas, according to the excellent work done by Dr. H. E. Box (1935 to 1955) who has recently changed the genus of some of the species concerned. Since all these species were previously referred to the genus *Diatraea* in the available literature, we are here considering them as such.

Here is an alphabetical list of the species involved, with the countries in which they occur, prepared according to data published by Box and the investigations of the author:—

### *Diatraea* species.

### Countries.

*albicrinella* Box

Brasil; British Guiana; Ecuador; Perú & Trinidad.

*b. busckella* Dyar & H.

Colombia; Panamá & Venezuela.

*canella* Hamps.

Grenada; the Guianas; Martinique; St. Lucia; St. Vincent; Tobago & Trinidad.

*considerata* Heinr.

Mexico.

*crambidioides* Grt.

United States.

*dyari* Box

Argentina.

*grandiosella* Dyar

Mexico & United States.

*guatemalaella* Schs.

Costa Rica; Guatemala & Mexico.

*impersonatella* Wlk.

Argentina; Brasil; the Guianas; Perú; Trinidad & Venezuela.

*magnifactella* Dyar

Mexico.

*minimifacta* Dyar

French Guiana; Trinidad & Venezuela.

*rosa* Heinr.

Venezuela.

*rufescens* Box

Bolivia.

*saccharalis* Fabr.

In all countries from the United States thru Central America, the Antilles and South America.

*tabernella* Dyar

Costa Rica & Panamá.

*veracruzana* Box (in litt.)

Mexico.

By the above list it will be seen that the species of widest geographical distribution, and at the same time responsible for the greatest amount of damage, greater than that of all other species combined, is the well known *Diatraea saccharalis* Fabr. which occurs from southern United States, through the Antilles, Central America, and the whole of South America, to the Province of Buenos Aires, in Argentina, where it is a pest of corn.

Due to the habit of the *Diatraea* larvae of burrowing into the stalks of the sugar cane as soon as it shoots out of the ground, being exposed only for a short time after hatching from the eggs—deposited in clusters on the leaves—when entering the midrib of the leaves, or the leafroll in their first feedings, it is easy to understand why the attempts to control the sugar cane borer by means of insecticides have not met with great success. It is questionable whether the expense of \$500,000 in insecticides, as reported by Dugas (1953) in Louisiana, for the control of the second generation of the sugar cane borer, in half of the infested area, was worth while if, when the crop harvest begun, the mean infestation of the sugar cane amounted to 28 per cent of the joints (Mathes *et al.* 1954) equal to that of the previous year, 1952, which according to Mathes *et al.* (1953) produced a loss estimated at \$9,000,000 for the State of Louisiana alone.

If these hardly convincing results were obtained in a region with well defined seasons, with frequent winters having freezing temperatures, where the borer can make only four generations per year, which can be easily timed by field observations, much less could be expected in the sugar-cane-growing countries of South America, where the borer multiplies freely the year around, having from five generations, as in Perú, according to Risco (1956a) to 12 generations per year, as in Cuba, according to Plank (1932).

On the other hand, the use of the natural enemies of the sugar cane borer, or biological control, is the method which has given practical control of the borer in the countries where it has been put to use, taking full advantage of its possibilities.

Since there are many natural enemies of *Diatraea* spp. in the countries where they occur, let us first distinguish between the egg parasites and larval parasites. At first sight it would appear that the egg parasites would be the most effective since they destroy the embryos of the borer before they can do any damage at all; but in practice this is not the case. To begin with, the recently hatched borer larvae are very feeble, and they are easily killed by natural causes such as rains, heavy dews and fogs, which added to their cannibalism accounts for a natural mortality of almost 90 per cent, according to the studies made by Pickles (1936) and Wille (1952). Then, if 90 per cent of the recently hatched borer larvae will die of natural causes, an egg parasite to be really effective should have to attack over 95 per cent of all eggs, which will be seldom possible.

The egg parasite, *Trichogramma minutum* Riley, was in use in the United States, Mexico, Perú and some of the Antilles against the sugar cane borer from 1930 to about 1950, but its use was discontinued (except in Barbados, B.W.I.), since no practical results were obtained, despite the numerous claims published.

Before entering into the discussion of the larval parasites of the sugar cane borers, let us pay a tribute to the entomologists who have undergone all sorts of difficulties and dangers in the hot and humid jungles of South America, looking for parasites of the borers, among whom stands out the late Dr. J. G. Myers (1931, 1935) a pioneer of biological control and to whom we are indebted for much knowledge and new parasites of the borers in South America. In 1932, 10 years before his untimely accidental death in Africa, he went on foot and in canoes through Northern Brasil, the Guianas and Venezuela, looking for them. This exploration gave us, among other things, the Amazon fly, *Metagonistylum minense* Towns., whose introduction from the lower Amazon into British Guiana in 1933, in which the author took an active part as Myer's assistant, has been an outstanding example of the possibilities of the biological control of the sugar cane borer.

To Box (1953b), we are indebted for the knowledge of many species of *Diatraea* in the Americas as well as for their host plants and for many new records of their

parasites, work which undoubtedly induced him to publish his list of the sugar cane insects of the world.

We have to mention also the contributions of Jaynes (1933), Cleare (1939), and Harland (1937), who have contributed with fundamental studies on the parasites of *Diatraea* or their artificial multiplication, initiated by the author (1930) with the study of the biology of *Lixophaga diatraeae* Towns., the Cuban fly.

The list of known larval parasites of *Diatraea* in the Americas comprises about 30 species, almost equally divided between Diptera and Hymenoptera, but of these, only three dipterous parasites have been extensively used for the biological control of the sugar cane borers.

These three dipterous larval parasites of *Diatraea* are the tachinids, *Lixophaga diatraeae* Towns., *Metagonistylum minense* Towns., and *Paratheresia claripalpis* v.d.W. Their remarkable superiority over all the other parasites of *Diatraea* may well be due to their natural ability for seeking their hosts, as proven by the high parasitization they attained, as well as by their mode of reproduction; depositing living maggots instead of eggs at the entrance of the tunnels made by the borers, and to the high biotic potential of *Metagonistylum* and *Paratheresia*, which are known to have up to 600 embryos, or to the short life cycle of *Lixophaga*, which can make it in 25 days.

Let us consider them separately to see what they have accomplished.

#### *Lixophaga diatraeae* Towns.

This parasite, known also as the Cuban fly, is a native of the Great Antilles, Cuba, Puerto Rico, Hispaniola and Jamaica, and was considered by Myers (1931) as the most efficient parasite of *Diatraea* known. It is a specific parasite of *D. saccharalis* and while occasionally it has been reared from *D. lineolata* Wlk., the corn borer, all attempts to rear it from other *Diatraea* have failed, and it is not known to have been reared from any other host.

It can be said that the utilization of natural enemies for the biological control of the sugar cane borer in the Americas, started 41 years ago, when in 1915, U. C. Loftin (24) of the United States Department of Agriculture was sent to Cuba to collect *Lixophaga* puparia for introduction into Louisiana (see Holloway et al. 1928). Several introductions were made from 1918 to 1920 (Holloway 1938) as well as in 1926 and 1927 (Jaynes 1938), but these introductions were not successful, because the biology of the parasite was not known at the time. After this point was elucidated by the author (1930) as well as the method for its artificial multiplication published by the author (1932), *Lixophaga* was successfully introduced into Antigua and St. Kitts in 1932, by Box (1935a), who improved the technique. From 1938 to 1944, it was introduced into Florida by the author (Scaramuzza and Ingram 1942) where its artificial rearing for the biological control of the sugar cane borer has continued over the years in at least one big plantation, the Felsmere Sugar Company, with good results as published at various dates and it is mentioned in the Yearbook of Agriculture of the United States Department of Agriculture, 1952, Insects.

*Lixophaga* has been introduced into several other countries and has become established in Perú (Scaramuzza 1952), Brasil (Gallo 1952), and some of the Lesser Antilles, with varying degrees of success but so far only in Antigua, St. Kitts and Cuba has given commercial control of the sugar cane borer, *D. saccharalis*.

In Cuba, where the author is in charge of this work for the Compañía Azucarera Atlantica del Golfo (which produces over half a million Long Tons of raw sugar in normal years) since 1945, the borer infestation was reduced from about 16 per cent average joint infestation at the time the work was begun, to about 4.0 per cent in 1948 (Scaramuzza 1948), thus amounting to a reduction of over 70 per cent in four years. This reduction has been maintained over the years, with small variations, due mainly to the fluctuations of our climate or to meteorological phenomena such as the cyclone of October 1948 (Scaramuzza 1949), which practically destroyed the *Lixophaga* population in the zone crossed by it.

Besides the two laboratories of the Compañía Azucarera Atlantica del Golfo, which produce over 60,000 *Lixophaga* flies each season, there are in Cuba several other entomological laboratories belonging to different sugar companies and one that belongs

to the Ministry of Agriculture, located at the Sugar Cane Experiment Station, at Jovellanos.

*Metagonistylum minense* Towns.

This tachinid is a native of the lower Amazon, in Brasil, where it was discovered by Myers (1935) in 1932, attacking the sugar cane borer, *D. saccharalis*, in a native habitat, the wild grasses on the banks of the Amazon River in the vicinity of Santarem. Its introduction into British Guiana in 1933, and its artificial multiplication there by Cleare (1939) is one of the outstanding achievements in the biological control of the sugar cane borer. Later, in 1934, Box (1938) was able to introduce it in St. Lucia, where *Lixophaga* had failed, also with great success, obtaining a very quick establishment of the parasite.

But the most remarkable achievement of this parasite is its establishment in Venezuela, accomplished under Box's able direction in 1950-51 (see Box 1953), where in 1953, according to private communications, it was attacking successfully four species of *Diatraea*, viz., *D. saccharalis*, *D. rosa*, *D. b. busckella* and *D. impersonatella*. At one farm in the State of Aragua, where the damaging species are *D. saccharalis* and *D. rosa*, the original joint infestation of 16.5 per cent, in 1952, was reduced to 7.6 per cent in 1955, a reduction of 56.3 per cent in three years.

*Paratheresia claripalpis* van der Wulp

This parasite occurs from Mexico to Argentina, through Central America as a parasite of several species of *Diatraea* and other lepidopterous larvae, as well as of some curculionids (Coleoptera) showing a wide host preference in different countries which led to a long synonymy. We are indebted to Dr. F. I. van Emden (1949) of the Commonwealth Institute of Entomology, for having clarified it for us, and now it is accepted that the great majority of forms found in the Americas belong to the species *P. claripalpis*, with a number of geographical "races" or strains, to explain the differences in host preference.

The attempts to use this important and widespread parasite of *Diatraea* were begun in 1928 when Jaynes (1933) of the United States Department of Agriculture was sent to Argentina and Perú to study and collect this and other parasites of the sugar cane borer for introduction into Louisiana.

*Paratheresia* has been introduced or transferred from one region to another in several countries by a number of entomologists, but nowhere has it been established permanently.

It was left to Perú, one of its native countries, to prove its efficiency for the biological control of the sugar cane borer *D. saccharalis*. In 1951, following Box's (1950) recommendations made in 1949, the author went to Perú at the invitation of the Sugar Producers Committee to direct a campaign for the biological control of the sugar cane borer. The *Lixophaga* fly was first introduced (Scaramuzza 1952) and, although soon established in one of the valleys of the coast, at Hacienda Laredo, near Trujillo, it failed to become established elsewhere despite the large numbers liberated. After two years, in October 1953, it was decided to change from *Lixophaga* to *Paratheresia*, the native parasite, which had been closely studied in the meantime with the idea of its future utilization.

The work in Perú is in charge of S. H. Risco, Agronomical Engineer, under the supervision of the author, who makes annual trips to Perú. In 1954, Risco published an interesting monograph on the subject.

As a result of this change, during 1954, there were liberated in Perú over 266,000 *Paratheresia* flies, covering about 28,900 acres of sugar cane, which represents about 90 per cent of the total sugar producing cane area of Perú. The benefits of these liberations are evident in the whole area, as the parasitization increased more than 50 per cent and consequently, the infestation was reduced by 61.3 per cent, in four years, according to a report published by Risco (1956). At Hacienda Laredo, according to the monthly report for February 1955 (Risco 1955), the reduction has been greater, since from 19.29 per cent average joint infestation for 1950-51, it was reduced to 5.39 per cent in 1954-55, a reduction of 72 per cent.



It has been said by various authors that it was not possible to increase the efficiency of a native parasite, by its artificial multiplication, once it has attained a certain degree of equilibrium with its host. Our experience proves otherwise, as exemplified by the results obtained with *Lixophaga* in Cuba, and with *Paratheresia* in Perú, both indigenous parasites of the said countries.

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# Local Dependence of Parasitic Insects and its Importance for Biological Control

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## ABSTRACT

From the fact that every species of organism needs specific environmental factors arises a different local (=biotope) dependence of host and parasites. Studies have been made with reference to this problem 1953-1956 at Berlin and its eastern surroundings. Each of the four host-species, studied (caterpillars or pupae of: *Anarta myrtilli* L., *Mamestra persicariae* L., *Evetria resinella* L. and *Acronycta aceris* L.) showed different qualitative and quantitative or only quantitative parasitization at different localities at the same time. Concerning the problem of biological control of insect pests these results are of importance for a) to favour parasites, b) import or export of parasites and c) to examine the effect of biological control.

It is a well known fact that in general it is only possible to breed a part — in most cases a very small part — of parasitic Hymenoptera and Diptera known up to now from an insect species, if this species is examined at a certain time and a certain place.

For example the *Catalogue of Parasites and Predators of Insect Pests*, prepared under the direction of Dr. W. R. Thompson, enumerates 38 species of parasitic Hymenoptera and five species of parasitic Diptera bred from larvae and pupae of the pine moth, *Bupalus piniarius*; however, I was only able to breed six species of parasitic Hymenoptera and four species of parasitic Diptera from the larvae and pupae of this pest, collected during 1952 and 1953 in the pine woods on the east side of Berlin.

On looking for the reason for this one finds that there may be three kinds of barriers preventing a parasite from existing in all places where its host exists:

*Topographic barriers* are present, if the host has been able to overcome, either by wandering or by human influence, seas, mountains or deserts, whereas this would have been impossible for the parasite.

*Climatic barriers* are present, if host and parasite in consequence of their different adaptation to climatic factors have different areas of distribution, which only coincide partly with each other. This part of coincidence can fluctuate according to the climate.

*Biocoenotic barriers* are present, if even within the above-mentioned area of coincidence the host lives together with its parasite only in a part of its biotops. The parasite needs for its existence another combination of environmental factors to that of its host and only finds this combination in a part of the host biotops.

With regard to the kind of such biocoenotic barriers one may imagine for example that an ichneumonid species needs lepidopterous larvae living on pine trees as hosts for its hibernating generation and lepidopterous larvae living on well defined herbs in pine woods as hosts for its summer generation. In this case the ichneumonid species would be only able to parasitize the pine pest in such types of pine woods in which the herbs (necessary for the hosts of the summer generation of the parasite) also grow.

As a result of such different local dependence of host and parasite there is to be expected a difference between the parasitization of a host species at a certain biotope and the parasitization of the same host species at another biotope at the same time. This difference could be qualitative and quantitative or only quantitative, quantitative in any case: a parasitic species reaches, as every organism species, its maximum density only in one type of biotope, namely in the one offering it the most favourable environmental factors. In other types of biotope it reaches smaller density the less favourable the environmental factors are.

On the occasion of the breeding of parasitic Hymenoptera and Diptera from lepidopterous larvae and pupae in former years, studies have been made with reference to the above-mentioned problem of local dependence of parasitic insects. For this purpose first the territory of research, the town of Berlin and its eastern surrounding, was

divided up into types of vegetation, which means types of biotops or also types of biocoenoses. On this basis some frequent species of Lepidoptera were examined as to their parasitic insects. The results are contained in the following four tables.

TABLE I. *Anarta myrtilli* L., 1955/56.

Parasites	Locality					
	dry		fresh		moist	
	1	2	1	2	1	2
from larvae:						
<i>Banchus volutatorius</i> L.	—	—	3	5	—	—
<i>Microplitis ruricola</i> Lyle	7	7	17	7	—	—
<i>Euplectrus bicolor</i> Swed.	—	—	2*)	3*)	2*)	1
						1*)
<i>Campylochaeta inepta</i> Mg.	—	—	3	1	2	3....
<i>Actia tibialis</i> R.D.	—	—	1	2	1	—
from pupae:						
<i>Labrorychus tenuicornis</i> Grav.	2	8	4	10	6	—
Host imagines	3	4	9	8	10	4
Proportion						
	parasites					
	host imag.					
	30	38	33	35	11	10
	10	10	10	10	10	10

\*) numbers of larvae parasitized by *Euplectrus bicolor*.

Discussion of Table I: *Anarta myrtilli* is a noctuid living on *Calluna vulgaris*. Its larvae were collected in July 1955 at six localities belonging to three types of biotop, here named “dry”, “fresh” and “moist”. Thus to each of these three types belonged two single localities.

Table I, like the following ones, contains all species of parasites bred from host individuals of at least two single localities.

As can be seen, the ichneumonid, *Labrorychus tenuicornis*, was living in all three local types: “dry”, “fresh” and “moist”. The tachinids, *Actia tibialis* and *Campylochaeta inepta*, as well as the chalcid, *Euplectrus bicolor*, were living in the local types “fresh” and “moist”. The braconid, *Microplitis ruricola*, was living in the local types “dry” and “fresh” and lastly the ichneumonid, *Banchus volutatorius*, was limited to the local type “fresh”.

From the standpoint of the local types the number of parasitic species bred from *Anarta myrtilli* amounted to two in the type “dry”, four in the type “moist” and six in the type “fresh”.

In addition to the qualitative difference there were also distinct quantitative differences of parasitization, as can be seen from the proportion: number of parasites / number of host imagines.

TABLE II. *Mamestra persicariae* L., 1955.

Parasites (from larvae)	Locality			
	sand		mud	
	1	2	1	2
<i>Phryxe nemea</i> Meig.	18	15	1	2
<i>Enicospilus ramidulus</i> Steph.	2	3	7	6
Host imagines	39	40	15	20
Proportion				
	parasites			
	host imag.			
	5.1	4.5	5.3	4.0
	10	10	10	10
Proportion				
	Tachinids			
	Ichneumonids			
	90	50	1.4	3.3
	10	10	10	10

Discussion of Table II: *Mamestra persicariae* is a very frequent noctuid living in Germany in gardens and fields. Its larvae were collected in September 1955 in four gardens within the city of Berlin, belonging to two local types, divided here as "sand gardens" and "mud gardens".

As shown in Table II, in this case the rearing only resulted in quantitative differences of parasitization .

It is conspicuous that the density of the tachinid, *Phryxe nemea*, was greater in sand gardens whereas the density of the ichneumonid, *Enicospilus ramidulus*, was greater in mud gardens. The proportion: number of tachinids / number of ichneumonids in sand gardens was about 70 to 10 against 2 to 10 in mud gardens.

TABLE III. *Evetria resinella* L., 1956.

Parasites (from pupae)	Locality			
	lichen- pine wood		bilberry- pine wood	
	1	2	1	2
<i>Actia nudibasis</i> Stein	4	2	5	3
<i>Glypta incisa</i> Grav.	26	17	4	7
Host imagines	68	24	73	52
Proportion				
	parasites host imag.			
	4.4	7.9	1.2	1.9
	10	10	10	10
Proportion				
	Tachinids Ichneumonids			
	1.5	1.2	12.5	4.3
	10	10	10	10

Discussion of Table III: *Evetria resinella* is the well known tortricid in Europe causing resinous galls on pine trees. These resinous galls, containing the pupae of the pest, were collected in the spring of 1956 in four pine woods, belonging to two local types: "lichen pine woods" and "bilberry pine woods".

From Table III it is obvious again that the differences of parasitization here were only quantitative. The total degree of parasitization in the "lichen pine woods" was much greater than in the "bilberry pine woods", while the portion of tachinids was — on the contrary — much greater in the "bilberry pine woods" than in the "lichen pine woods".

TABLE IV. *Acronycta aceris* L., 1953 and 1955.  
Percentage of Parasitization by *Compsilura concinnata* Mg.

	1953		1955	
Single trees	1.2	2.2	1.2	2.9
A few trees together in streets or courtyards	5.0	7.5	5.5	
Trees in parks	15.5	24.4	15.4	20.5

Discussion of Table IV: In the last five to ten years there has been a remarkable outbreak of the noctuid, *Acronycta aceris*, on horse-chestnut trees (*Aesculus hippocastanum*) in the city of Berlin, whereas only a few individuals of this pest could be found in the surrounding of Berlin.

It was striking that the damage was always much greater on single trees in the courtyards of houses than on trees in parks. Therefore, three local types were distinguished: single trees in courtyards, a few trees together in courtyards or streets, and trees in parks.

Virtually the only parasite bred from *Acronycta aceris* larvae was the tachinid, *Compsilura concinnata*.



Table IV shows that the degree of parasitization of *Acronycta aceris* on trees in courtyards and streets was very much lower than on trees in parks, in both years, 1953 and 1955. From this it is to be seen that the local differences of parasitization of a host species are also temporarily constant.

Summarized, the results show that the parasitization of a host species is different at the same time in different biotops. With this the problem of the local dependence of parasitic insects (or, in other words, the problem of biocoenotic differentiation of parasitic insects) is settled. The chief question to be answered in the future is the cause of this differentiation.

Concerning the biological control of insect pests the problem of biocoenotic differentiation of the parasites is of importance in three directions:—

1) To favour parasites. The differences in local dependence of a parasitic species ascertained by means of comparison of localities, enables us to study the causes of these differences and to use the results to favour the parasite by influencing the environmental factors.

2) For import or export parasites. The comparative study of localities offers the possibility of recognizing quickly and surely the host dependence of a parasitic species and so to find out the parasites with the greatest host dependence and the smallest local dependence for the purpose of exporting to another country.

3) To examine the effect of biological control. From the above it is seen that in the case of an examination of the effect of biological control, whether after import or to favour a parasitic species, only biocoenotically equal localities can be compared with each other as to the density of this parasitic species.

#### DISCUSSION

ALVAH PETERSON. When you have a complex of parasites attacking a given host, do you usually find that one species is more important than the others?

W. SCHWENKE. It changes from case to case. In the case of *Acronycta aceris*, the tachinid, *Compsilura concinnata*, has been far more important than the others.

# Biological Control of the Fall Webworm, (*Hyphantria cunea* Dr.), in Europe

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## ABSTRACT

The fall webworm, a new pest for Europe, was introduced from America fifteen years ago. At the Vienna conference in February, 1952, organized by the European Organization for Plant Protection, it was decided to initiate a project for the biological control of the fall webworm in Europe. A far-reaching scheme for the biological control of this insect by means of introducing American parasites into Yugoslavia was undertaken with the financial aid of FAO and the Yugoslav Government.

During the years 1953-55, the following parasites were received from Canada: *Hyposoter fugitivus fugitivus* Say., *Hyposoter pilosulus* Prov., *Campoplex validus* Cress., *Rogas hyphantriae* Gahan, *Meteorus hyphantriae* Riley, *Meteorus bakeri* C. and D., *Apanteles hyphantriae* Riley, and *Mericia ampelus* Wlk.

The adults, reared from cocoons received from Canada and those reared in our laboratory at Zemun, Yugoslavia, were released in heavily infested places where no other control measures had been nor will be taken. The first release was during the summer of 1954. The same autumn the cocoons of the liberated parasites were found but in the following spring and summer none could be found. It was most probable that the liberated species had not hibernated, for lack of intermediate hosts. Therefore, in 1955, the work has been concentrated on finding out new hosts of American parasites.

*M. ampelus* was specially investigated and particularly in relation to the silkworm. At the conference of EOPP at Jouy-en-Josas, France, March 17, 1955, it was decided not to proceed with colonization of this tachinid until the possibility of its becoming a parasite of the silkworm was fully investigated. Experiments during 1955 have demonstrated that it is unable to develop in silkworm caterpillars and the release of this parasite in the field will be possible in the spring of 1956.

The appearance of the fall webworm, (*Hyphantria cunea* Dr.), in Europe attracted the attention of European entomologists, particularly those in countries where the pest was observed. The comparatively quick spread, great potential power of propagation with two complete generations annually, and the large number of cultural and forest trees, which are attacked by this pest, has engaged a great deal of our entomologists' researches in recent years.

The fact that the fall webworm has many enemies in its natural home in America led European entomologists to the conclusion that it would be worthwhile to attempt the biological control of the fall webworm by introducing and acclimatizing the most active species of American parasites in Europe.

During the years 1953 to 1955, the Food and Agricultural Organization provided funds to the Commonwealth Institute of Biological Control in Canada for collecting and sending American parasites of the fall webworm to Yugoslavia. The Yugoslavian Government provided money for a special laboratory and for experts and assistants. F.A.O. also provided funds for the training of Yugoslav experts for this task in foreign countries and furnished the above-mentioned laboratory with necessary equipment.

## SHIPMENT OF AMERICAN PARASITES DURING 1953 TO 1955

The first shipments of American parasites arrived the end of July and beginning of August and the last ones the end of September and beginning of October. All parasites were forwarded as cocoons. In 1953, the cocoons were put in flasks and these fastened to the inner walls of a wooden box, and in 1954, the cocoons were put immediately into wet moss. In both cases the result was a high mortality, not only of the imago emerged during the journey, but also of the pupae in cocoons. However, all the imperfections were successfully removed during 1955. Special wooden boxes,

constructed and used for the first time for this purpose at the European Laboratory of Biological Control, Feldmeilen, Zurich, Switzerland, (Delucchi, Tadic and Bogavac, 1954) were used for the shipments of parasites.



Fig. 1. Laboratory of Biological Control at Zemun (near Beograd).

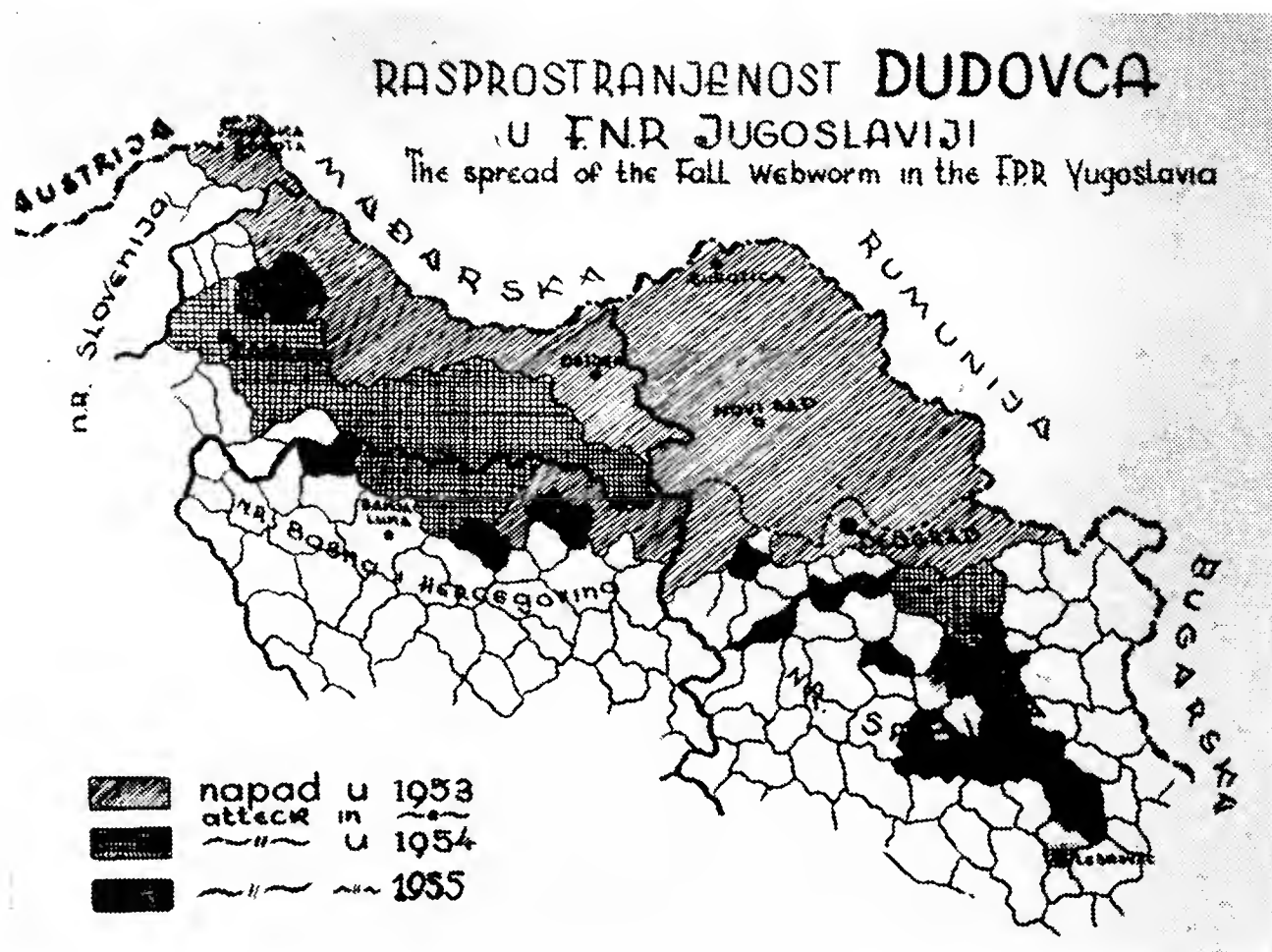


Fig. 2. Spread of the fall webworm in Yugoslavia (1953-55).

In the above-mentioned three-year period, the following species of parasites were received: *Hyposoter pilosulus* Prov., *H. fugitivus fugitivus* Say, *Campoplex validus* Cress., *Rogas hyphantriae* Gahan, *Apanteles hyphantriae* Riley, *Meteorus backeri* C. and D., *M. hyphantriae* Riley, and *Mericia ampelus* Wlk.

#### INVESTIGATION OF THE BIOLOGY OF AMERICAN PARASITES

In the laboratory at Zemun, investigations on the biology and behaviour of American parasites were carried out, and appropriate methods for their mass breeding



developed. During this work some interesting observations concerning the biology of the parasites were made. According to Tothill (1922), *M. ampelus* has only one generation in Canada, whereas we have reared three complete generations in the laboratory. A similar case was recorded with *Campoplex validus* Cress. If we add to this the fact that even the fall webworm develops two complete generations, and, in some years, a partial third, whereas in Canada it has but one generation, it is possible to conceive the differences that take place in the development of the above-mentioned parasites. Climatic differences between Canada and southern Europe influenced these differences in development, both of the host and its parasites. In the course of the work on the acclimatization of American parasites, it became obvious that it was necessary to have secondary hosts of European origin and in connection with this, the hibernation of the parasites under new conditions represents the fundamental problem of the whole scheme. In spite of a whole series of experiments, we did not succeed in discovering a method for mass breeding of some species of American parasites. In such cases we restricted ourselves to the release of imagoes from cocoons obtained from Canada.

*Hyposoter fugitivus fugitivus* Say and *H. pilosulus* Prov.

When the investigation of the biology of this species had been successfully concluded and the problem of their mass propagation solved, an attempt was made to find a European host on which this parasite could develop and hibernate. Experiments demonstrated that this parasite can develop only in *Stilpnotia salicis* L. and *Dicranura vinula* L. The first host was found in Yugoslavia during the last two years, only in small numbers, attacked by a virus disease, and the second one was quite rare, with the result that neither could be practically utilized for mass breeding.

*Campoplex validus* Cress.

This is the only species on which biological and mass breeding experiments are still under way. Two interesting points are worth mentioning: First, the impossibility for this species to develop in the gipsy moth caterpillars, although the American literature indicates this pest as a host; and, second, the existence of two and perhaps three generations during the vegetative period in Europe. This parasite hibernates in the cocoon as a mature larva.

*Rogas hyphantriae* Gahan.

The biology of this species and a method for its mass breeding were established in the first year of our work. The question of the hibernation of this monophagous parasite is still not understood in Europe or in Canada.

*Apanteles hyphantriae* Riley.

In 1954, it was observed that this species is an egg parasite of the fall webworm and the next year (1955), we reared this species to the adult stage on eggs of the fall webworm. The female of the parasite lays her eggs in the embryo of the host and the mature larva leaves the host caterpillar when the latter is in the fourth stage. The mass breeding of this species in the laboratory is difficult and the problem of its hibernation has not been solved (see M. Tadic paper "*Apanteles hyphantriae* Riley, an egg parasite of the fall webworm": a separate paper given at the Tenth International Congress of Entomology).

*Meteorus backeri* C. and D. and *M. hyphantriae* Riley.

Since it was impossible to breed this species under laboratory conditions, adults were reared from cocoons, shipped from Canada and released.

*Mericia ampelus* Wlk.

The relation of this tachinid to *Bombyx mori* (L.) had first to be established to avoid parasitism of this valuable species in Europe. Experiments during 1954 and 1955 showed that the larvae of this tachinid parasitizes the silkworm caterpillars, but they cannot develop in them beyond the second stage. Thus, the first release of this tachinid was made in the spring of 1956. Since *M. ampelus* hibernates in the host cocoon, acclimation and mass breeding are not difficult. However, the problem of asynchroni-

zation between this parasite and the fall webworm still represents a serious problem. If this attempt proves unsuccessful, this question could, perhaps, be solved by introducing *M. ampelus* from southern regions of North America.

### RELEASE AND ACCLIMATION OF AMERICAN PARASITES IN YUGOSLAVIA

The first releases of American parasites were carried out during August and September, 1954, in Vojvodina, where there are many plantations of mulberry trees and fruit trees and the attack of the fall webworm is rather heavy every year. In addition, authorities proclaimed this small village an experimental area and no control measures will be carried out in it for the duration of investigations. The following species were released: *Hyposoter* sp., *Rogas hyphantriae* Gahan, *Meteorus* sp. and *Apanteles hyphantriae* Riley.

Our efforts to find the cocoons of these parasites in the spring of 1955 and 1956 were unsuccessful. It is clear that released parasites did not hibernate and we tried to find the causes. According to American literature, the eight species of parasites we have received have 54 hosts in America. However, only two of these hosts occur in Europe: the gipsy moth and the fall webworm, and among the other hosts the same genera do not appear in Europe. Thus, the only possibility for their acclimation in Yugoslavia lies in their acceptance of new secondary hosts of European origin, which would enable them to hibernate.

The experience gathered during the first two years directed our work on the release of American parasites in 1955 somewhat differently. In that year release was in Serbia and near Zemun, in the neighborhood of Beograd. By releasing the parasites in these three different biotopes, we wished to offer them as great a variety of entomofauna as possible, hoping that they would succeed in finding an interim host for hibernation.

The results obtained so far show that the hibernation of American parasites and the detection of European secondary hosts represent the most serious problems to be solved in the work on the acclimation of American parasites of the fall webworm in Europe.

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# *Apanteles hyphantriae* Riley, an Egg Parasite of the Fall Webworm

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## ABSTRACT

In the course of the project for the biological control of the fall webworm in Yugoslavia (1953-56), *Apanteles hyphantriae* Riley was imported from Canada. This species with a very interesting biology was investigated in the Laboratory of Biological Control at Zemun, Yugoslavia.

In a series of tests, that have been carried out with this species in the course of the last three years, it has been established that *A. hyphantriae* is an egg parasite of the fall webworm. The copulation of *A. hyphantriae* follows immediately its eclosion, but oviposition begins at the room temperature (20-25°C.) five to six days after eclosion. The females lay eggs in the eggs of the fall webworm. The embryonic development of the parasite lasts about 48 hours. During this time the size of the egg increases two to three times. The larva hatches while still in the embryo of the fall webworm so that the hatched caterpillar is already parasitized. The total development of the parasite in the host lasts 26 days.

In carrying out the scheme for biological control of the fall webworm, *Hyphantria cunea* Dr., in Europe, among several other parasite species, *Apanteles hyphantriae* Riley was introduced from Canada and the United States of America. This species having an interesting development has been the object of investigations in the laboratory of biological control at Zemun, Yugoslavia.

The representatives of the genus *Apanteles* are well known and have been much utilized in the biological control of noxious insects, chiefly as larval parasites (Frost, 1942). As far as I know, no representative of this genus has proved to be an egg parasite. By a series of recent experiments, it has been established that *A. hyphantriae* is an egg parasite of the fall webworm. I say "egg parasite", but, in fact, it is a parasite both of eggs and of caterpillars, for the female of *Apanteles* lays her eggs in the host eggs and the parasite completes its development in the host caterpillar as with *Ascogaster*, *Chelonus* and *Phanerotoma*. In the literature, for instance, we find a detailed description of *Ascogaster carpocapsae* Viereck (Cox, 1932) and Zorin observed in 1929 that *Microgaster marginatus* Nees lays eggs in the eggs of *Polia oleracea* L. 24 hours before they hatch. Tothill (1922) says "... The egg of this species of *Apanteles* has not been seen and cannot be described. ... No female flies have been observed depositing eggs but something of the process can be learned from a study of the reproductive system" and also goes on to state "The egg, now fertilized and bathed in fluid, passes into the base of the ovipositor and in an instant becomes planted in the general body cavity of a fall webworm larva ... that the fluid is not in this case a poison is clear from the fact that victimized caterpillars remain healthy for days and weeks after being attacked."

In this short paper I am going to dwell chiefly upon the explanation of data obtained from the investigation of the oviposition and the embryonal development of *A. hyphantriae*.

## COPULATION AND OVIPOSITION

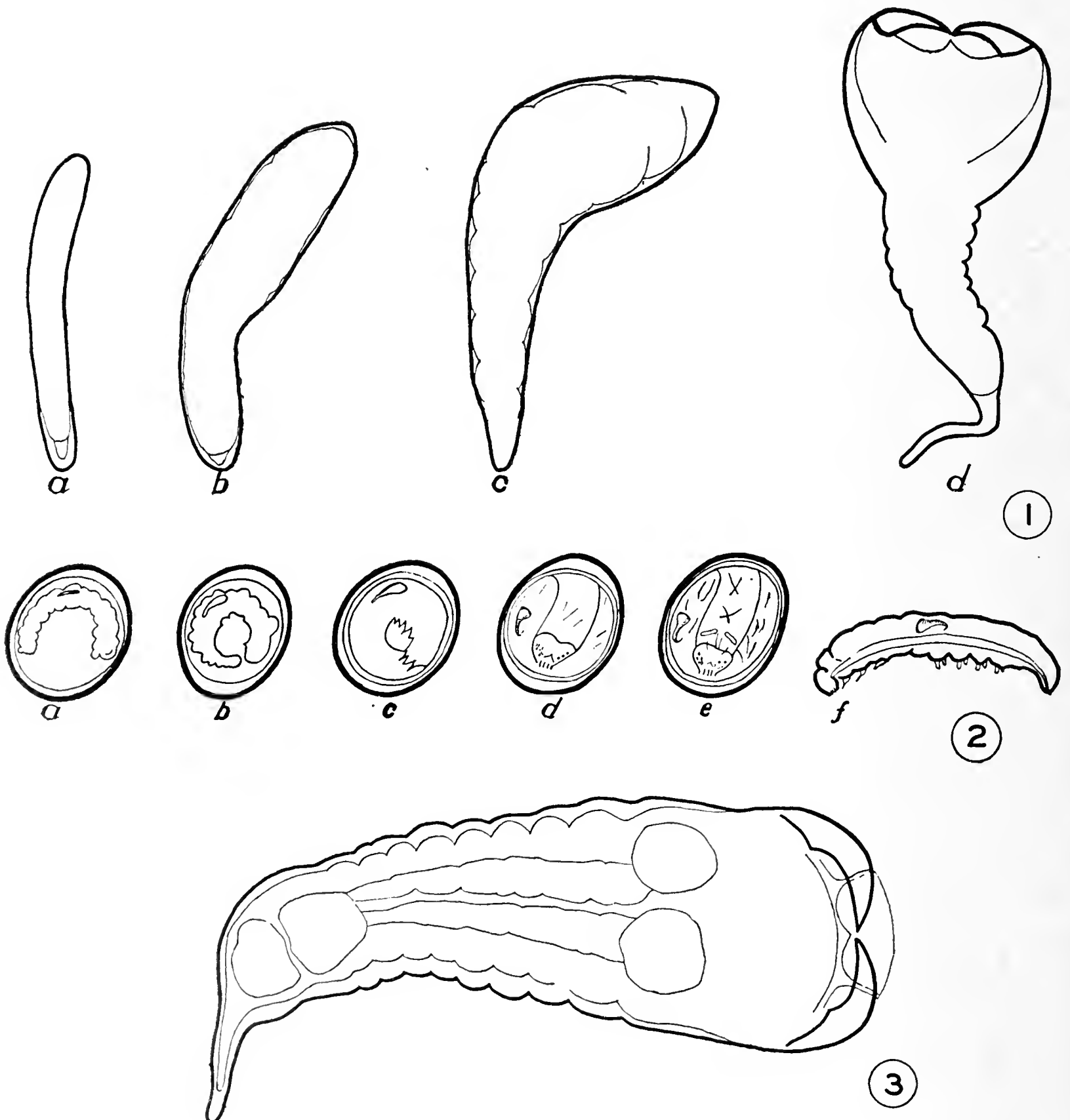
The rearing of adults of this parasite, under laboratory conditions, is very difficult. The adults usually fly for several days in the breeding room. They were fed a solution of honey, pollen and food according to Parker's formula (honey, sugar and agar-agar) and vitamins. The breeding room was aerated. Copulation was observed only once in a glass cylinder immediately following emergence. For this reason I isolated 60 cocoons individually in vials and reared the males separately from the females in special cylinders. In this way the copulation was artificially retarded for four or five days. After that, I shut a male and a female in a smaller vial in which the copulation could easily be observed under a binocular. In such circumstances they would usually copulate at the first contact. The duration of the copulation was less than one-half a minute. The mated

females pass over the egg clusters of the fall webworm piercing the eggs with their ovipositors. Each insertion of the ovipositor is not always followed by oviposition. Two parasite eggs may be laid within a host egg but only one parasite matures. Unfertilized females laid eggs in the same manner as fertilized ones. The female stays on the host's egg, while ovipositing, not more than 10 to 15 seconds and immediately afterwards passes to the second and so on. When the females of *A. hyphantriae* were offered eggs of the silkworm and of the gipsy moth, they did not parasitize them. The female oviposits in all ages of host eggs.

### EMBRYONIC DEVELOPMENT

The fall webworm females laid their eggs on a thin sheet of paper in the cage. The egg clusters thus obtained were cut in several pieces and each was put in a separate vial with a mated female. By successive fixings of these parasitized eggs, material for investigations was obtained.

The female parasite oviposits her eggs usually into the middle part of the embryo, between the intestinal tract and the skin. The embryonic development unfolds quickly and after 24 hours' time the differentiation of the embryo can be observed; after 48 hours the embryo is formed and hatching begins. Consequently, the whole embryonic development of *A. hyphantriae* occurs in the embryo of the fall webworm within 48 hours. This development is schematically represented in Figs. 1 and 2.



The egg of *A. hyphantriae* is morphologically similar to eggs of other *Apanteles* species but is somewhat smaller. It is 0.9 mm. long and 0.1 mm. wide. During embryonic development, the egg increases its volume two to three times.

In the course of dissection of parasitized eggs of the host, I observed several times that the egg of *Apanteles*, which had been laid outside the embryo, did not begin its development, although the eggs deposited into the embryo of the same age were already hatched. In the same way the dissection showed that the yolk of a fall webworm egg, which had not been fertilized and did not develop, contained two eggs of *A. hyphantriae* that did not develop.

#### POSTEMBRYONIC DEVELOPMENT

Hatching of the egg of *A. hyphantriae* takes place in the host embryo so that the young fall webworm caterpillar already contains the parasite. The larva of *Apanteles* is semicircular. During the first larval stage the larva migrates towards the posterior part of the caterpillar and at the end of the first-stage can be found under the malpighian tubes. The larva does not attack the organs of the caterpillar and it probably feeds only on fat tissue, blood and lymph. The development of the larva in the first-stage lasts usually about ten days. Its characteristic feature is the large size of its head in comparison to the small body and the short tail (Fig. 3). The head is square and the body becomes narrower towards the anal segment. On the dorsal side, the larva has on each segment several spines as long as the segment itself and bent towards the tail. The colour of the larva is pale yellow, almost transparent. Before passing into the second stage, the larva loses its tail. The number of larval stages is not known.

After completing its development, the larva leaves the host through an opening, which is usually made laterally on the caterpillar of the fourth-stage, and spins a white cocoon near it. The total development of *A. hyphantriae* within its host lasts about 26 days under laboratory conditions.

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← Fig. 1. Embryonic development of *A. hyphantriae* Riley (schematically represented). a, egg immediately after oviposition; b, egg 24 hours old; c, egg 48 hours old; 4, larva just after hatching.

Fig. 2. Embryonic development of *A. hyphantriae* Riley in the egg of the host (schematically represented). a, immediately after oviposition; b, after 24 hours; c, after 48 hours; d, after 72 hours; e, after 96 hours; f, after 120 hours.

Fig. 3. Larva of *A. hyphantriae* Riley in the first-stage (schematically represented).



# A Review of Recent Work on Nematodes Associated with Insects With Regard to Their Utilization as Biological Control Agents<sup>1</sup>

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## ABSTRACT

*Recent contributions to the study of the association between nematodes and insects are reviewed. Many of these contributions are of a taxonomic nature, but sufficient data have been obtained concerning the bionomics of the association to suggest that its future study will be advantageous to the theoretical and applied aspects of entomology.*

Nematodes that have insects as primary hosts are of interest to biological control work. There are many such species and they belong to nine families in four orders of Nematoda. Oldham (1933) was one of the first to propose the use of nematodes as biological control agents, though earlier workers, particularly Cobb, referred to the possibility. Sweetman reviewed the work up to 1936, and Steinhaus the work up to 1949. The first field experiments were recorded in 1940 by Glasser, McCoy, and Girth.

In general the taxonomy of the nematodes is difficult. This is especially so in nematodes associated with insects for the parasitic mode of life often modifies the morphology of the species. The scattered nature of the observations also contributes to the confused state of the taxonomy. A useful reference has been the section of Filipjev's (1934) book, or its later English translation Filipjev and Schuurmans Stekhoven, (1941). Goodey's monograph (1951) is also of value. Fortunately recent investigators have examined the taxonomy of these families and their contributions are noted in the following brief review of these nine taxonomic groups.

Members of the Rhabditidae usually have a phoretic relationship with insects in that their dauer larvae, or resting stage larvae, are attached to the insect cuticle. Many new rhabditids of this type were described by Sachs (1950). An exception to this habit was described by Körner (1954) who found a species that inhabits the body cavity of a lueanid. Rühm (1954) described a species parasitic in the hind gut of bark beetles. Osehe (1952) made a much-needed revision of the genus *Rhabditis*, and Dougherty (1953c and 1955) has examined this revision from the nomenclatorial viewpoint.

Another important family is the Steinernematidae. All species of this family are associated with insects. The host is usually infected by eating a dauer larva. The nematode eventually enters the haemocoel where it reproduces and causes the death of the host. Recently, three new species, *leucaniae*, *bothynoderi*, and *carpocapsae* were assigned to the genus *Neoaplectana* by Hoy (1954), Kirjanova and Puchkova (1955), and Weiser (1955) respectively, bringing the total of recorded species in this genus to nine.

Likewise many of the members of the Diplogasteridae have a phoretic relationship with insects. Hirschmann (1952) gave new records of diplogasterids with dauer larvae attached to various aquatic beetles. Körner (1954) identified a diplogasterid found attached internally to the genital segments of beetles, a characteristic often recorded earlier, and recently by Théodoridès (1949). Körner also recorded a diplogasterid from the trachea of two cerambycids. Sachs (1950) described several diplogasterids from dung beetles. With the exception of three species described by earlier workers, the members of this family do not appear to harm their hosts.

The fourth family in the Rhabditina that has insect associates is the Cephalobidae. There are two subfamilies, the species of which show a phoretic relationship with the host and apparently cause it no great harm. Körner described a new species from *Spondylis buprestoides*, and Hirschmann (1952) a species from two carabids and an elaterid. Rühm (1954) also recorded species of *Panagrolaimus* on bark beetles.

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Stammer and Wachek (1952) proposed a new family, Carabonematidae, in the Rhabditina. They described a new genus, *Carabonema*, for a new species found in the body cavity of five species of carabids. This eelworm appears to be parasitic and causes the death of the hosts.

Both superfamilies of the Tylenchida have species associated with insects. In the Tylenchoidea the host is usually invaded by a fertilized female, which develops in the host body cavity and produces eggs or larvae. The larvae leave the host, mature, mate, and infect other host individuals. There are variations in this pattern, but in most cases the gonads of the host are damaged. Wachek (1955) re-examined members of this superfamily and assigned 33 new species and three new genera to it. Rühm (1954) added a new genus, and described species associated with insects in the Tylenchidae (1955c) and Neotylenchidae (1955b).

In the superfamily Aphelenchoidea the eelworms show a greater diversity in their associations with insects than do the Tylenchoidea. Here, they may be either parasites in the body cavity and gut or commensals in the galleries of bark beetles. Wachek (1955) erected two new genera and transferred several genera to the family, among which the most notable is the genus *Sphaerularia* Dufour, 1837. Rühm (1956) has described many new species and genera in this superfamily as well as in the previously described groups. His publication has appeared just recently and is a most comprehensive study of those nematodes associated with bark beetles.

In the Oxyuroidea there are two families and a subfamily that contain species associated with insects. These eelworms usually infect the host in the egg stage and attain maturity in the insect gut, apparently without harming the host. Many species are described in the literature, but there is little data on their life-history or bionomics. Recent contributions have been made by Baylis (1946), Basir (1948), Serrano Sanchez (1945, 1947) and Théodoridès (1953). Mention should also be made of Dollfus' (1952) monograph on the Oxyuroidea of Myriapodes. Basir is also preparing a monograph on the group.

The last group is the Mermithoidea composed of the Mermithidae and the Tetradonematidae. Adult Mermithidae are free-living but the larvae are parasitic in the body cavity of the insects. They frequently damage the host gonads, and usually kill their hosts upon emergence. The taxonomy of the group is complex, but Polozhentsev (1953) has given some aid in providing a check list of the known species, as well as describing two new genera (1952). Schuurmans Stekhoven and Mawson (1954, 1955) described five new species. Goodey (1941) described a new genus and species in the Tetradonematidae.

Records of insect nematode associations have been found in most of the Orders of insects. Unfortunately no up-to-date list of insect-nematode associations exists, though the period up to 1946 was covered by the list of van Zwaluwenberg (1928) and La Rivers (1949). Partial listings were made by Polozhentsev (1954) for Russian records, and Théodoridès has provided lists for bark beetles (1950a), geotrupids (1950b, and 1952b), and with Jolivet (1950) for chrysomelids. More records appear to have been published in the last 10 years than in the period before 1946.

For biological control purposes three groups, Steinernematidae, Tylenchoidea, and Mermithidae, are the most interesting. Most of the species of these kill or impair the reproductive capacity of their hosts, whereas in the other groups this behaviour is limited to certain species of nematodes.

It is therefore interesting to note the role that these particular groups play in the natural control of insect populations. Hoy (1954) recorded that 26 of 104 larvae of a crambid (Lep.) were infected with *Neoaplectana leucaniae* Hoy. Kirjanova and Puchkova (1955) recorded average infections of *Neoaplectana bothynoderi* Kirjanova and Puchkova in a weevil that ranged from 13.3 to 67.5 per cent in different localities and types of crop culture. Records of parasitism by the Tylenchoidea are numerous. Wachek gave a range of 2.5-22.5 per cent for *Heterotylenchus bovienii* Wachek in a carabid in three localities in an eight month period. Infections of similar magnitudes are recorded for tylenchoids in bark beetles by Rühm (1954a) in Germany and by Massey (1956) and Moore (1955) in the United States. There is a suggestion that in

most insects mermithid infections may follow a pattern similar to that recorded by Gendre (1909) for mermithids in mosquito larvae. This pattern consists of a high degree of parasitism in a small localized area. Recent observations have verified this with regard to mosquito larvae. Muspratt (1945) described infections of 70-80 per cent in approximately one in each 10 localities in which the host occurred, Jenkins and West (1954) recorded infections of up to 100 per cent in certain pools but no infections in neighbouring pools, and Stabler (1952) found 90 out of 217 specimens infected in one area. With other insects, Polozhentsev (1952) recorded a reduction of 60 per cent in the population of cockchafers in a Russian wood; Artyukhovski (1953) recorded 15-60 per cent parasitism in *Porthetria dispar* (Linné) in an area in Russia, and Crowcroft (1948) recorded a parasitism of 51 per cent in earwigs in Tasmania. These figures suggest the occurrence of high infections localized in small areas similar to the pattern with mosquito hosts.

The few examples cited above suggest the role which nematodes play in controlling insect populations. The use of nematodes, however, requires more information on their ecological relationships with insects to be of value in biological control considerations.

A knowledge of the specificity of nematodes for a particular host is essential. Evidence on this can be drawn from observations in nature, supplemented by data from experimental work. Hoy (1954) found *N. leucaniae* occurring naturally in a noctuid and a crambid, but in laboratory experiments he was able to infect nine species of melolonthids, and species of elaterids, asilids, and weevils. Dutky and Hough (1955) recorded a similar wide range of experimental hosts for a species of *Neoaplectana* found in the codling moth. These observations suggest a wide range of hosts for the species of this genus, but this is not completely true for *N. glaseri* Steiner has only been successfully infected in a few scarabeids, weevils, and melolonthids. Little evidence is available on the host range of the Tylenchoidea. The literature suggests that they are fairly specific but may infect related host species or species of closely related genera. Rühm (1955a) examined this question from the viewpoint of using nematode parasites to elucidate problems in bark beetle taxonomy. Observations for the mermithids are conflicting. Older records suggest a wide range of hosts, but Baylis (1944) was able to infect only earwigs among a series of hosts tested with *Mermis nigrescens* Dujardin. Rathke (1953) found *Hexamermis albicans* (v. Siebold) to occur in only two species of snails though other suitable and previously recorded hosts were present in the habitat.

The searching and dispersal attributes of a parasite are important in biological control work. Nematodes that infect in the egg stage probably depend on chance for their spread through the host population, much as do bacteria and fungi. Those nematodes which have an infective larval stage apparently seek or are attracted to a host (Bovien, 1937), but it is unknown to what extent. Presumably, most nematodes are spread by the movements of their hosts, as has been demonstrated for various species of *Neoaplectana*. Parasitized hosts, however, may be hindered in their flight or movement, though this remains to be investigated. These points suggest why nematode parasitism may reach high percentages but remain localized.

There is a lack of any numerical data in the literature to show the relationships that exist between nematode parasitism and the density of insect populations.

More attention has been given to the effects of the physical or abiotic factors on nematode parasitism. Moisture is essential for nematodes and most observations are centered on its importance. Hoy (1955) suggested that moisture deficiencies prevented the development of *N. glaseri* in New Zealand. Kirjanova and Puchkova (1955), however, found no clear relationships between soil moisture and the parasitism of *N. bothynoderi*. Wachek discussed the effect of abiotic factors on the Tylenchoidea and concluded that they have little effect except in species that have long free-living periods. Rühm (1954) investigated the effect of abiotic factors on the nematodes of bark beetles. Couturier (1950) observed the necessity of moisture for mermithids in the laboratory and suggested that this limited their use as control agents. Rathke (1953) concluded that the weather determined the period of mermithid growth within snails, and the number of worms per host. Théodoridès (1952a) drew attention to the fact that most records of mermithid parasitism come from areas of chalky soils. Useful as

these data are, much additional work is required for a fuller understanding of the effect of the physical environment on the nematodes parasitic on insects.

Competition between nematodes and insect parasites or pathogens apparently has not been investigated in recent work. Oldham's observation (1935) that only 0.12 per cent of 3,400 insects examined had both hymenopterous and eelworm parasites suggests that there may be an antagonism between eelworms and insect parasites.

It appears from the literature that insecticides do not affect parasitism by nematodes. The numerical data of Kirjanova and Puchkova (1955) show no appreciable differences between infections on control plots and plots sprayed with two concentrations of insecticide.

The ability to culture a parasite is important in biological control work. Nematodes can be bred on hosts in the insectary, and two successful attempts in culturing them *in vitro* have been recorded. The success with *N. glaseri* is well-known in this regard. Lately Stoll (1948-1954) has conducted further researches in culturing of *N. glaseri*. Hoy (1954) has also succeeded with *N. leucaniae*. Dougherty, in a series of papers (see 1953a and b), was successful in culturing several free-living species of *Rhabditis*. This research is of interest because of its possible application to nematodes associated with insects. No *in vitro* cultures of mermithids or Tylenchoidea have been recorded.

Many students of biological control are acquainted with Glaser, McCoy, and Girth's (1940) experiments with *N. glaseri*. Recently, a new development in the utilization of this nematode was recorded by Dumbleton (1945) with the introduction of the eelworm into New Zealand for control attempts against various native melolonthids. Hoy (1955) recorded that the nematodes were liberated in 1952 and recovered in 1953, but he found no overall reductions in the host populations compared to the controls. He attributed this lack of success to a number of factors and stated that new attempts will be made under more favourable conditions. He also recorded that shipments of *N. glaseri* have been sent to Wallis Island, near Samoa, South Pacific, for use against the coconut weevil, but no information is available on the results of these tests.

A new development in this work was the report by Dutky and Hough (1955) of a *Neoaplectana* sp. and an associated bacterium found in codling moth in the United States. The nematode apparently acts as a carrier for the bacterium which is fatal to the host. The nematode feeds on and reproduces in the decomposed tissue of the host. Kirjanova and Puchkova (1955) probably observed a similar phenomenon with *N. bothynoderi*, for they record that the nematode gave off a peculiar substance that caused the body of the host larva to become soft and filled with a pasty contents of a rose yellowish colour. It is unknown if Weiser (1955) found a bacterium associated with his *N. carpocapsae* from the codling moth. Dutky and Hough stated that further work is in progress, and it will be particularly interesting to learn the results.

It is hoped that this review will give some idea of the advances that have been made in this field during the last 10 years. The work is still in its infancy, and Sweetman's concluding remarks in his review of 1936 that "nematodes should be studied further as a knowledge of the life-histories and ecological relationships are decidedly lacking with most species" is almost as applicable today as it was 20 years ago.

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# Observations on the Parasite Complex of *Choristoneura* (*Cacoecia*) *murinana* Hb. (Lepidoptera: Tortricidae)

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## ABSTRACT

During the investigation on the parasitization of *C. murinana* Hb. in the Vosges in 1955 24 species of parasites and hyperparasites have been reared, 9 being first records for this host. Observations are given on the frequency, ecological preferences, and of the phenology of the main parasites. The results are compared with the data of other authors.

The following observations on the parasitization of the European fir budworm, *Choristoneura murinana* Hb., were made in the Vosges in 1955, where parasite collections were undertaken by the European Laboratory of the Commonwealth Institute of Biological Control for shipments to Canada to be used against the related Canadian spruce budworm, *Choristoneura fumiferana* Clem. The researches were carried out in different ways. First, field collected larvae were reared in the laboratory by the same methods previously used by Bucher (1953) in 1947/48. Secondly, field collected pupae were segregated, according to the sampling dates and localities, to assess phenological and ecological differences in the pupal parasitism.

The pupae were collected from undergrowth trees as well as from the crown region of mature firs. Finally, trials were made to verify the dates from the fractionated rearings, by direct field observations of the main parasite species.

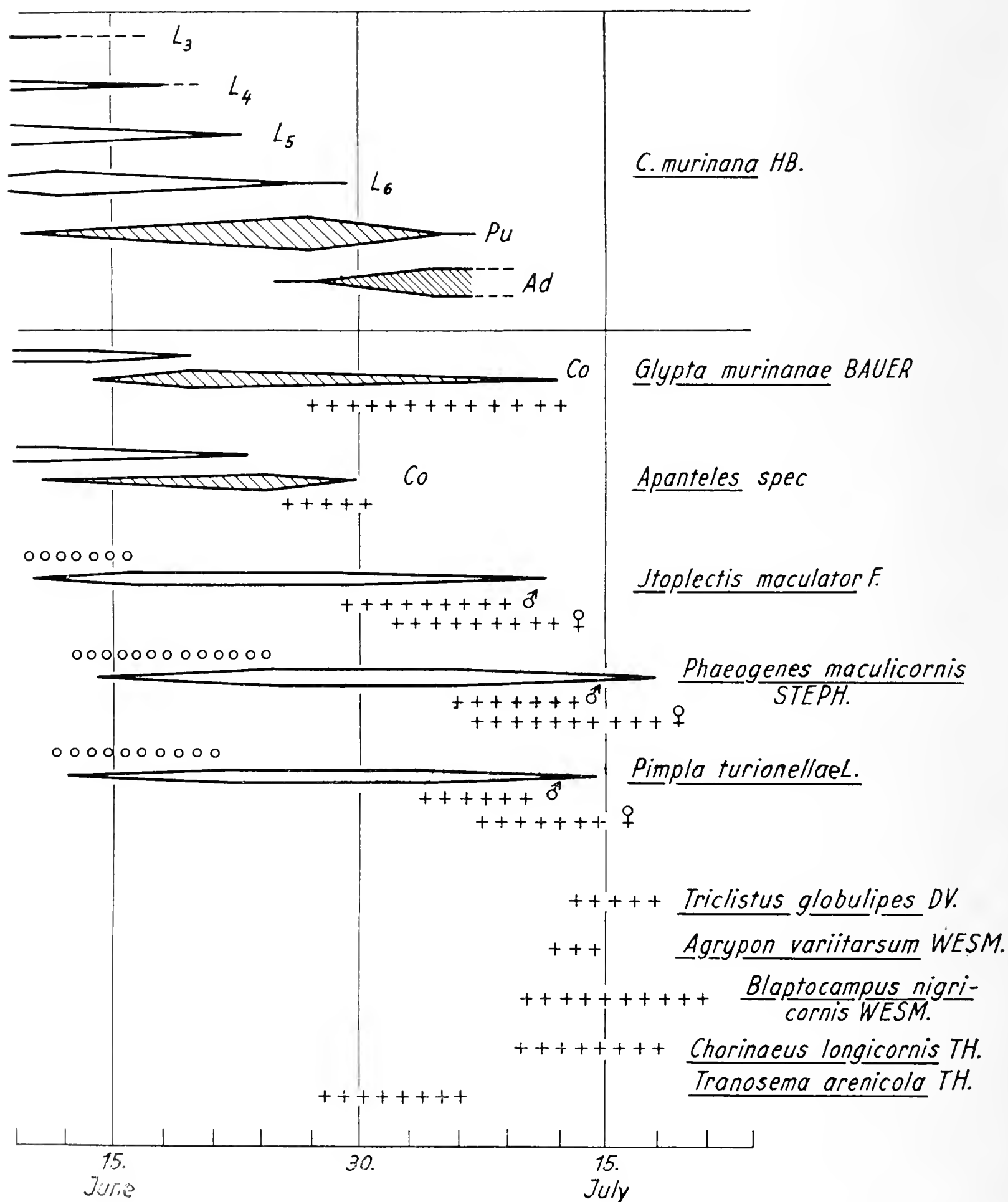
The researches were carried out in the vicinity of Pépinière near Ribeauvillé (Ht. Rhin) in France, in a district already investigated by Bucher (1953) in 1947/48. There a more or less continuous area of infestation of *C. murinana* was to be observed, with single small foci, where the firs (*Abies alba* = *A. pectinata*) lost up to 70—80% of the current needles. In general, the intensity of infestation was not as severe as in 1947/48. During the first half of June, when the fir budworm was mainly in the 5th and 6th larval instar, temperatures were low and almost every day rainfall occurred. Later on, weather conditions became more favourable. Pupation of *C. murinana* commenced by June 11, emergence started by June 25 and was practically finished in the first week of July<sup>1</sup>.

In 1955, 24 parasite species were reared from *C. murinana*. The following are first records of parasitism on that host: *Glypta* sp., near *cicatricosa* Ratz.—the life habit of this ichneumonid is similar to *G. murinanae* Bauer. *Blaptocampus nigricornis* Wesm.—this ichneumonid species attacked larvae VI and pupae and emerged from pupae, the duration of its development was about 25 days. *Amblymerus subfumatus* Ratz.—this common hyperparasitic chalcid was reared from the cocoons of *Apanteles*. *Nemorilla floralis* Fall.—a tachinid, attacking the larvae and emerging from pupae. *Actia maksymovi* Mesn.—another tachinid, emerging from full grown larvae, was hitherto only known as a parasite of larch tortricids. *Chorinaeus longicornis* Thoms.—an ichneumonid which attacked larvae VI and pupae and emerged from pupae. *Tranosema arenicola* Thoms.—an ichneumonid, emerging from larvae VI. *Mesochorus* sp., near *vittator* Zett.—a hyperparasitic ichneumonid. *Apanteles murinanae* Capek and Zwölfer — Braconidae.

The degree of larval parasitism varied in 1955 between 2%—7%. Among 480 larval parasites examined, *G. murinanae* had a frequency of 85% and was the predominant species. *Apanteles* was represented by 5%. All the remaining larval parasites together constituted only 10%. Pupal parasitism amounted in 1955 from 29% up to 55% with an average of 42% (in 1956 = 33% — 40%). Within the group of pupal parasites the different species showed the following relative frequencies: *Phaeogenes maculicornis* Steph. = 49%, *Itoplectis maculator* F. = 34%, *Pimpla turionellae* L.

<sup>1</sup>The results of the 1955 work have meanwhile been fully supported by the observations in the Vosges in 1956.

= 5%, *Triclistus globulipes* Desv. = 4%, *B. nigricornis* = 2%, *C. longicornis* = 2%, *Agrypon variitarsum* Wesw. = 1%, Tachinidae and remaining ichneumonid species together = 2%.



An evaluation of the results of the different rearings and direct field observations demonstrated considerable differences in the ecological preferences of the individual parasite species. While the degree of parasitization in the thickets of young firs was only slightly smaller than in the crown region of mature stands, the composition of the parasite complex was quite a different one. *G. murinanae* occurred about 4 times more frequently in the crown region of open mature stands than in dark or dense stands, or on young firs. In the trunk and crown region of mature firs, *P. maculicornis* was dominant, while *I. maculator* was in second place. On young trees, however, *I. maculator* was much more numerous than *Phaeogenes*. *T. globulipes*, *A. variitarsum*, *B. nigricornis*, *Ch. longicornis*, and the parasitism by a *Hexamermis* sp. (Mermithidae) was practically restricted to thickets of young firs. Thus, the parasite complex reared

from hosts from young trees was found to be richer in species, but of somewhat less effectiveness, than that associated with host populations living in the crown region of mature firs.

The deciding period for the attack of the main pupal parasites is during the first half of the pupal period of the host. Therefore rearings, which shall establish quantitatively the pupal parasitism of *C. murinana* should not commence earlier than 15 days after the appearance of the first host pupae. Fig. 1 demonstrates the dates (Vosges 1955) of parasitization, of the larval period, and of the emergence of the more important parasite species in connection with the host phenology.

The development of *Glypta* and *Apanteles*, as had already been pointed out by Franz (1940) and Bucher (1953), is largely synchronized with the development of the host. In 1955, both the parasites were hyperparasitized very much. *Apanteles* showed a mortality of about 40%, mainly due to parasitism by *Hemiteles areator* Panz. and probably *H. albipalpus* Thoms. and by *A. subfumatus*. Twenty per cent of the *Glypta*-population was also killed by hyperparasites. Those were *Monodontomerus aereus* Walk. and *I. maculator*. The two species emerged from the cocoons of *Glypta*. At least the Ichneumonid *I. maculator* must have attacked *Glypta* already within the larvae of *C. murinana*. Both the species can operate also as primary parasites. The hyperparasitization of *Glypta* by the important pupal parasite *I. maculator* must be considered as a phenomenon of competition between the univoltine group of parasites (*Glypta*, *Apanteles*) and the multivoltine group, comprising the pupal parasites. Another factor of mortality in *Glypta* is the exposure of the cocoons to predacious insects. In 1955 larvae of *Chrysopa*, and adults of a species of Nabidae (Hemiptera) were observed attacking *Glypta* cocoons.

As it doesn't seem opportune to draw conclusions about the role of the parasite complex as a control factor of *C. murinana* from results obtained during a single observation period, and from only one locality, the observations were compared with previous investigations of Schimitschek (1936) in the Vienna Forest and (1943) in southwestern Moravia, with those of Kolubajiv (1934) in southwestern Moravia, with those of Franz (1940), who observed the infestation in the Southern Black Forest, and finally with those of Bucher (1953), who studied the biotic control factors of *C. murinana* in the Vosges and in the Northern Black Forest during 1947/48.

When we compare the parasite lists, published from the different observation areas, we find, that the parasite complexes reared in the Vosges and in the Black Forest exhibit a close relationship, which is evidently due to the fact, that these areas are only separated by the Rhine Valley. The parasite list from the Vienna Forest is based only upon a small number of reared hosts, but we can comment, that the correspondence of this list with those of the Vosges and the Black Forest is greater than the correspondence with the parasite list from southwestern Moravia. Both the Vosges and the Black Forest are situated in the maritime influenced climatic region with a rather oceanic climate, while the Vienna Forest lies at the boundary of the Pannonic-Continental climatic region. The parasite complex reared by Kolubajiv (1934) and Schimitschek (1943) in southwestern Moravia, which belongs more or less to the continental climatic region, exhibits a somewhat exceptional position. It is very rich in species, since a total of 45 parasite species have been reared, whereas during both the investigations of the Vosges infestation only 33 species were observed. About 50% of the Moravian parasites of *C. murinana* have not been noticed from the other observation areas. Compared with the frequency of the Ichneumonidae, the Chalcididae and Tachinidae have been represented in a much greater number of species in the Moravian infestation. The tachinid, *Blondelia nigripes* Fall., for example, was stated by Kolubajiv to be "very frequent". This is the only case known, in which a tachinid showed a greater importance as a parasite of *C. murinana*.

Concerning the general order of effectiveness and regularity of occurrence of the individual parasite species, a comparison of the investigations, so far published, shows, that among the larval parasites *G. murinanae* is almost regularly present and also generally predominant. Among the pupal parasites, *I. maculator* was dominant in five of seven examples, being only twice in the second place. *P. maculicornis*, in spite of

its irregular occurrence, is mentioned as very frequent in three reports and was in two examples the most important pupal parasite. *Apechthis resinator* Thunb., *A. rufata* Gmel. and *B. nigripes* occasionally appeared at the 3d and 4th place of the parasite lists. The other parasite species were recorded in all the reports to be only scarce.

Summarizing the different works on the reduction of the *C. murinana* population by its parasites, we find that, apparently in consequence of the different sampling techniques applied, the statements about the larval parasitism show great differences, varying between 1% and 26%. Here, further studies, using mainly field cages as applied by Franz (1940), seem to be commendable. As to the pupal parasitism, in which the host alternating parasite species are involved, the wide host range of the majority of these species seems to grant a certain bulk of parasites, which as a rule are able to kill 20-50% of the remaining host population. The particular importance of the multivoltine pupal parasites within the complex of controlling factors may be seen in the fact, that these species attack the host in its numerically weakest position, and consequently reduce that part of the host population, which had succeeded in escaping from the other mortality factors.

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# *Sphaerularia* spp. (Nematoda: Allantonematidae) Infesting Bumble Bees and Mountain Pine Beetles in Canada

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## ABSTRACT<sup>1</sup>

*This is the first authentic record of Sphaerularia bombi Duf. found parasitizing bumble bees in Canada. The parasite was collected from the abdominal cavity of Bombus terricola Kby. queen and B. ternarius Say. queen from Saskatoon, Saskatchewan.*

*A new species, Sphaerularia hastata, is described from the mountain pine beetles Dendroctonus monticolae Hopk. and D. pseudotsugae Hopk., and the cocoon of a hymenopterous parasite, Coeloides dendroctoni Cush., from Steamboat Mountain, British Columbia.*

<sup>1</sup>Manuscript to be published in the Canadian Journal of Zoology.





# On Biological Pest Control

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## ABSTRACT

Biological pest control by support or by introduction of natural enemies (predators), parasites, or infectious diseases of the species in question as a rule will only keep it down. Extermination of a noxious species is then possible only within a limited area: if its enemies prevail, and if there is no fresh immigration from the outside. More especially an explosive increase of the population will never be prevented by the natural enemies of the injurious species, because their increase is only a consequence of the increase of the pest itself. The increase in the population of the controlling agent, therefore, always occurs too late, i.e. at a time when a catastrophe has already struck, the enemy profiting from it belatedly.

Bird protection, as generally applied, is based on erroneous premises. Birds will not prevent mass increase of injurious insects; only later will they profit from the abundance of food. As birds are not adapted to preying upon definite species of insects, the abnormally increased number of birds will keep down all insects, upon which they feed without discrimination. This may lead to the extermination of rare species.

Limited control, not extermination, of an imported pest is to be expected, if its enemies, parasites, or infectious diseases are introduced from its country of origin. If these were able to fully control the injurious species, they would have exterminated it already at home.

Full control, i.e. extermination of an introduced or native pest species, is possible only if it is brought into contact with an organism which it has not met before, and against which it has not developed a protective mechanism. If such an organism is found, it will always be necessary to make sure that it will not develop into a pest itself, after it has destroyed the original noxious species. Introduction of the controlling species has to be sudden, and the number of introduced individuals has to be sufficiently large, in order to prevent the noxious species from learning to avoid the new enemy, or to develop strains which are resistant to the parasites or infections, i.e. to prevent the development of biocoenotic balance between the species to be controlled and the controlling agent.

Biological pest control existed in the days of primaeval human culture when man accumulated stores. In his homes and store rooms, in order to keep down injurious commensal rodents, he kept representatives of the Mustelidae and Viverridae, and later on a species of the family Felidae, originally maintained for cultic reasons; this eventually developed into the domestic cat (*Felis catus catus* L.).

However, methodical control of unwelcome animals is a modern way. The first step was the protection of insectivorous birds. In order to have them effectively destroy the injurious insects in an agricultural area, their existence within this zone was promoted by various means. At this time the necessity of this type of bird protection for increased crop production is generally recognized. However, the expectations set on the results of bird protection appear to be at least exaggerated, and the results are frequently inadequate. I became aware of this fact 40 years ago, when I had an opportunity to see the conditions prevailing in Syria and Asia Minor. In these countries cats in the villages often are more numerous than people. The cats are not fed; it is, therefore, easily understood that no birds can settle in these areas without being devoured by the cats. According to European concepts, as there are no birds at all, insect pests should overrun the fields of the peasants; but this is not true: the harvests are perfectly normal. As a matter of fact it does not appear that in other countries mass increase of insects has ever been prevented by birds. An example is the recurrent overrunning of vegetable plantings by the caterpillars of the cabbage-butterfly (*Pieris brassicae* L.) in Central Europe, where there is a numerous bird population. The real facts are that,

to start with, there is a mass increase of the noxious insects. This supplies sufficient food to the birds which feed on them, so much that they may add another brood, or increase the number of eggs. Then, when the increase of the pests stops, but not that of the insectivorous birds, the birds turn to other sources of food, or they migrate into a more favourable territory. This means that the increase in the number of individuals of the birds follows that of the pest; it does not prevent it.

Anyway certain effects are produced by bird protection, i.e. an one-sided promotion of one single group of animals. It has frequently been calculated how many insects are destroyed by one single bird. Under natural conditions the bird, with a certain amount of selection, will devour everything in its way of eatable animals that it can obtain, and with complete disregard of the functional importance of the respective animal for human agriculture or forestry. As a rule rare species are less able to withstand decimation of their number than more common ones. I am inclined to explain, as a consequence of the overwhelming populations of birds, the strong reduction or disappearance of a considerable number of rare species of insects in several parts of Central Europe within the last 50 years<sup>1</sup>. Common species, and these include the pests, are much less endangered in this respect. Also there are never enough birds to prevent an eventual explosive increase<sup>2</sup>.

If, however, bird protection will not work in the expected manner, the idea of promoting enemies of our pests is essentially correct. Storage, increased planting of certain crops, or other measures, may inadvertently produce a mass increase of certain animal species. Because they participate in the use of values created, man, against his own will, has upset the natural balance in favour of the pests; and these, under the new conditions have developed greatly increased populations. Obviously it is necessary to reestablish this balance by making more difficult the living conditions of the pests by additional interference with their environment. It appears logical to promote natural enemies, parasites or infections. Measures of this kind have been widely, and successfully, applied in biological pest control. They are well known, and need not be discussed in detail. By methodical use of natural enemies, parasites, and infections, it is often possible to reduce the populations of the pests, and to keep such species under control. But as a rule complete extermination cannot be expected. The explanation is that such agents would have exterminated the pest long ago. As regards to parasites a certain amount of resistance is developed with time and a certain host-parasite balance is established. Only locally in a more or less restricted area is it occasionally possible to fully exterminate a pest, under conditions when it cannot replace mass extermination by increased reproduction, i.e. if the environment does no longer support the existence of the species in question. Even in highly populous colonies of such concealed-living animals like termites it has been possible in northern India to control them efficiently in houses by introducing ants of the species *Monomorium salomonis* (L.) and *Solenopsis geminata* (Fabricius) into such buildings. These ants, which live in large colonies, soon control the termites<sup>3</sup>. Even in large territories ants that live in sizeable colonies often are able to control other animals upon which they feed. Every zoologist knows from experience that he will not find any other animals under stones where ants are living. In Germany K. Gösswald has recently pointed out the great importance for pest control of strong populations of the red forest ant (*Formica rufa* L.) within a forested area.<sup>4</sup> But even this species which, as a rule, is useful to man, may initiate unwelcome conditions, if the aphids which are favoured by these ants, become unduly numerous and ruin the young shoots of the trees.

<sup>1</sup> Within the 3 weeks that I now have been in Canada, and was able to see part of the provinces of Quebec and Ontario, I was struck by the scarcity of birds compared to conditions in Central Europe, and this in spite of numerous protective measures, especially in the national parks. Conditions in Canada apparently are less removed from the primitive status. (These observations were supported later on during my further stay in North America).

<sup>2</sup> This will not mean that I am against bird protection as such. But the motions for such protection should be clearly shown. Birds are well integrated into nature which is frequently mistreated by man. We like birds. The song of a bird belongs into a spring landscape. We should have the courage to admit, that we protect birds for ethical reasons, and that we are willing to apply nature protection not only for economical interests.

<sup>3</sup> Ants which may be a nuisance in houses, obviously are less dangerous than termites; also, if necessary, they can be more easily controlled.

<sup>4</sup> Gösswald, K. 1951. Die rote Waldameise im Dienste der Waldhygiene. Forstwirtschaftliche Bedeutung, Nutzung, Lebensweise, Zucht, Vermehrung und Schutz. Lüneburg.

The biological picture surrounding man is becoming increasingly less clear, because animal species are transported into foreign areas where many of them have become settled more or less permanently. For instance, because of the great influence which the Near and Middle East have had on the development of mankind, various native animals have become attached to man and transported as his commensals into all continents. Such species are the cockroach (*Blatta orientalis* L.), the cricket (*Acheta domesticus* (L.)), the yellow slug (*Limax* (*Limacus*) *flavus* L.), and the house-mouse (*Mus musculus* L.). In most recent times, because of worldwide commercial traffic which takes less and less time, this spread can be observed more and more. The improved heating of residential houses and storage buildings has made possible the permanent introduction of tropical species into temperate zones. As a rule such foreign species include the worst pests within an area. This may be because the species in question has found more favourable conditions, and, therefore, was able to reproduce abundantly. Possibly also it is more adaptable to man than commensals already present, or it may fill a gap within commensal populations. Moreover, frequently its most important natural enemies of its old home do not exist in the new territory, and it carries with it neither its parasites nor its infections. May I be permitted to quote a specific case from my own field of interest, one that, by the way, is not a pest. The case in question is that of *Potamopyrgus jenkinsi* (E. A. Smith), a fresh-water snail belonging to the Hydrobiidae, a family of streptoneuran gastropods, which has been introduced into Europe from the Southern Hemisphere, probably from New Zealand. As it will tolerate brackish water with a salt content of up to about 17 parts per thousand, it occasionally occurs in the area of the Central European sea coasts together with local indigenous species of the genus *Hydrobia* Montfort. These latter are frequently parasitized by various stages of different species of trematodes, the final hosts of which, probably in most cases, are seabirds. Many snails, thereby, are castrated, in certain places up to 90 per cent, whereas *Potamopyrgus* is not parasitized at all by these trematodes. Therefore, a considerable number of hydrobias are eliminated from reproduction, but all individuals of the introduced species are fully reproductive; this is the most important as *Potamopyrgus* reproduces parthenogenetically.

In application of biological pest control the usual method is the study of natural enemies, parasites and infections of a pest in the country of origin, in order later on to use them as control agents in the territory where the species has become noxious. I am of the opinion that such methods deserve only secondary consideration, as they are of minor importance. To start with it is not immediately known whether such a species is able to exist in the new territory. In this connection one may think of the failure of the experimental introduction of enemies and parasites of the North American Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) into France. Even if the introduction of an antagonist of the imported pest should have been successful, it would at most have kept down the pest population. If it could do more, it would have eliminated the pest already in the country of origin. It is also not very likely that an injurious species is just able to maintain itself in new territory, and that the mere introduction of a natural enemy would be sufficient to prevent it from resisting environmental influence; if this were true there would have been no mass increase nor any damaging effect. On the other hand the mass release of such a natural enemy or parasite which would eliminate the injurious species is practically impossible and economically not feasible. For instance I do not think much of a method of biological control applied recently against the giant landsnail, *Achatina* (*Lissachatina*) *fulica* Bowdich, originally an East African species, but now widely distributed in the countries around the Indian and Pacific Oceans, namely by means of an East African carnivorous snail, *Gonaxis kibweziensis* (E. A. Smith), a representative of the family Streptaxidae. This carnivorous snail, in its original African home territory, feeds on all kinds of worms and landsnails, including *Achatina fulica* Bowdich, but does not exterminate it. It can be assumed that the carnivorous species in new territory, as in the old, will feed on existing snails and worms, and may considerably increase if a plentiful food supply, such as that represented by a population of *Achatina fulica* Bowdich, is available. But there is no guarantee that the noxious species will become extinct.

If biological control is to lead to extermination of a pest I believe it would be more promising to look for enemies, parasites, or infections in countries where



the injurious species does not occur normally, and select such agents which it has not met before. It appears perfectly possible that by this method species can be found which will completely destroy the pest, and which it cannot avoid. If a parasite or infection is transmitted to the pest it acts destructively because no balance has been developed between parasite and host. As a contrast the example of African trypanosomiasis can be cited. This infection which is produced by several species of *Trypanosoma* (dependant from the part of Africa where *T. brucei* Plimmer and Bradford, *T. congolense* Broden, or *T. vivax* Ziemann occur) make it impossible to keep domestic livestock (cattle, horses, pigs, dogs), but it does not kill the wild ungulates of the country.

The basic idea of biological pest control is the assumption that man has upset the natural balance and has produced conditions which have promoted mass increase of the pests. Therefore the balance has to be upset in another direction in order to get rid of the pest again. Obviously control by natural enemies, parasites or infections which so far have not met the pest, can be effected against both native and introduced species. If there are difficulties in connection with the introduction or spreading of such a controlling species in the new environment one sometimes is able to intervene with protective measures. The Australian lady-bird, *Cryptolaemus montrouzieri* Mulsant, for instance, is used for control of species of the genus *Pseudococcus* Westwood on *Citrus* plants in California and in the Mediterranean area. In these new countries it sometimes will be damaged because the hibernating pupal stages die from frost; therefore these Coccinellids are raised artificially and afterwards turned out into the open in the early spring. If they are applied in large numbers there is a possibility to block the increase of the shield-lice.

If a desirable agent has been found, and if it has been proved that it will survive in a new environment, it will be necessary to find out what consequences are to be expected from its introduction. There is always the possibility that the introduced agent, after destruction of the original pest, might become adapted to the new environment and develop into a pest itself. It is also known that introduced control species have adopted a new mode of life in new territory. Therefore, it appears essential that problems of this kind should be directed by a central agency, and that introduction of foreign species by unauthorized persons should be prohibited.

If, however, after careful experimentation, a species has been accepted for biological control, its release should be sudden, and made with as great a number of individuals as possible. It is not impossible that an injurious species in time will learn to avoid a new enemy, or will develop strains which are resistant to introduced parasites or infections.

In general I believe it would be more effective to develop new enemies, parasites, or infections which have not met the pest species, than to try controlling a pest by its natural enemies. This would be much less expensive, although the scientific problems would be more difficult. Obviously, where no effective foreign enemies have been found, the natural enemies should be used where it is possible. But it is clear that in such a case the efficiency of control would be less. The method of biological control now proposed should be able to supplement the method of developing strains of plants which are resistant to pests. Both methods, together with chemical control, will supply effective protection against pests. It has to be considered that it often is advantageous if measures against noxious species are taken based on different assumptions, and with different methods, simultaneously or at a calculated interval. There is then a good chance that a pest that is able to avoid the impact of one method of control will not escape from another.



# Life-Cycle and Host-Parasite Relationship in the Field and the Larval Anatomy of *Metaphycus taxi* Alam

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## ABSTRACT

*Metaphycus taxi* exists concurrently with *Coccophagus taxi* as an endoparasite of *Eulecanium taxi* on yew tree (*Taxus baccata*) at Silwood Park, U.K. The ratio of parasitism of these parasites is 18:13. *M. taxi* and *C. taxi* are distinguishable in all stages. Coccids parasitized by them also possess distinguishable characters. *M. taxi* has two generations a year, though the host has only one. Adults of the two generations differ. Their behaviour in relation to host and their percentage of parasitism are also different. Each generation has a marked 'Pre-pupal' stage, and the larval duration of the second generation is greatly prolonged.

Laboratory experiments on photokinesis and phototaxis support the occurrence of higher percentage of parasitism in better illuminated regions of yew tree in the field. Host selection behaviour agrees with the prevalence of super and multi-parasitism in nature and may be considered analogous to the 'graded oviposition response' of *Ooencyrtus kuvanae* (Lloyd, 1938).

The fully-grown larva is elongated and subcylindrical with distinct head and thirteen segmented trunk region. The mouth-parts are highly specialized. The lumina of the mid and hind-guts are not in communication. The hindgut has no diverticulum which is distinctly present in Braconidae (Alam, 1952). Reduced number of ventral tracheal commissures and of ganglia on the ventral nerve cord suggest higher evolutionary status to Encyrtidae over Braconidae.

## INTRODUCTION

The genus *Metaphycus* Mercet is retained separate from *Euaphycus* Mercet and the species under observation is put as a new species in the former. The life-cycle of the genus *Metaphycus* in the field is not sufficiently studied. Imms (1918) collected good observations on the activities of *Aphycus melanostomatus* in the field. (Smith and Compere, 1928) had touched on the seasonal life-history of *Metaphycus lounsburyi*. Similarly, an account on the biology of *M. helvolus* is also available (Flanders, 1942).

*M. taxi* is for the first time recorded as an important parasite of *Eulecanium taxi*. The present paper is a concise but complete observation on the activities of the parasite in its natural environment. The host-parasite relationship has been given considerable emphasis. Some experiments on the host selection behaviour of adult parasite, in the constant temperature room, were carried out with encouraging results. Similarly, experiments were done on effect of light on the activity of adult parasite — a problem so far not studied on chalcids — and interesting results were achieved. The anatomy of the pre-imaginal stages, with special reference to the fully-grown larva, has been done.

## HABITS OF ADULT

*M. taxi* exists concurrently with *Coccophagus taxi* in the field. Their life-cycles run parallel with clear coincidence of their different stages. The ratio of parasitism of these parasites in the samples of the present writer was 18:13. Both species attack *E. taxi* which is well established on a yew tree at Silwood Park. At no stage of development these parasites resort to hyperparasitism but do form a good example of multi-parasitism not fatal to either.

Adults are commonly seen in the field from fourth week of May till the end of June and again from the last week of July till the end of August with some variations due to weather. They run swiftly on the twigs visiting both sides of the leaves in search

<sup>1</sup>I am highly grateful to Prof. O. W. Richards, Dept. of Zoology and Applied Entomology, Imperial College, London, U.K., for permission to work at Silwood Park (Field Station of the College) and for his useful suggestions on the problem.

of hosts but can not be easily detected owing to their minute size (1.27 mm.) and coloration. They fly quite frequently on bright sunny days. The parasite has two generations a year, but the percentage of parasitism of these generations do not show any wide difference. Smith and Compere (1928) have recorded three generations of *M. lounsburyi* annually at California.

In spite of very close biological similarities the adults of the two parasites can easily be distinguished, for *C. taxi* is black with a yellow pattern on the fronto-vertex while *M. taxi* is yellow. The pupae can also be easily distinguished, for a coccid containing *Coccophagus* is larger with the dorsum greatly arched and the host looks blackish while it is yellowish when parasitized by *Metaphycus*. It has been observed that darker areas of the tree (27.3, 21, 7.7 ft. candles as average intensities of light in fore-noon, after-noon and evening respectively) have a lower percentage of parasitism (21.6%) as compared with the percentage of parasitism (39.6%) in the better illuminated areas (64.8, 58.3, 18.5 ft. candles). This suggests that light has a stimulating effect on the activities of the parasite as has been shown later in light experiments.

### DISTINGUISHING FEATURES OF THE PARASITIZED COCCID

The different stages of *M. taxi*, except the egg stage, can be studied in the field without much difficulty. A host containing early larval stages generally shows circular or slightly oval dark brown patches. It is alive with the dorsum looking fresh and unarched. The third stage larva invariably kills the host and appears as a long, broad and mid-longitudinally lying dark brown patch and the dorsum of the host loses its freshness and becomes markedly arched. In the pre-pupal and colourless pupal stages the host looks brownish and has no trace of the mid-longitudinal patch. Instead, all along its posterior and lateral margins small dark brown pellets can be seen which are the larval faeces. The pigmented pupa gives smoky reflections if pigmentation has just started, while in advanced stage the reflections are those of the adult's coloration.

### FIRST GENERATION OF PARASITE

The adults of the first generation are prevalent from fourth week of May till the end of June, having developed from overwintering larvae. The egg-laying occurs through all this period. Generally more than one egg is laid in each host. The host is either in the late 2nd. nymphal stage or a young adult which has not yet started egg-laying. It has been observed that invariably the parasite's eggs fail to hatch if the host starts egg-laying shortly after parasitization. Such eggs are always encircled by some reddish matter showing that they are probably killed by phagocytosis. Compere and Smith (1932) and Cendana (1937) have also held a similar view on death of *Coccophagus* eggs. On the other hand, the hatching of parasite's eggs inhibits further activity of host's reproductive system.

The larval stages of the first generation are normally present in June and July. Generally five larvae per host are found, but as many as nine per host is not an uncommon number. In the beginning the larvae are haemophagous. Later on they feed on fat body and ultimately by the time they enter the 3rd. stage the sarcophagous habit results in death of the host. Pupation starts in July and continues till early August and the emergence occurring almost at the same period. The adults emerging at this time of the year form the second generation.

### SECOND GENERATION OF PARASITE

The adults of this generation are commonly present from the last week of July till the end of August. This is also the egg-laying period. The host invariably is in the early 2nd. nymphal stage, whereas, the 1st. nymphal stage is never parasitized. The adults of this generation never lay more than one egg per host and never behave as super- or multi-parasites. Hatching occurs before winter and hibernation of the parasite takes place in the 1st. larval stage. The host whether parasitized or unparasitized always undergoes hibernation in the 2nd. nymphal stage. By the following May the hibernating larvae either become fully-grown or have started pupation and the hosts are dead. The following differences between the two generations of the parasite are quite obvious: —

	First generation	Second generation
Eggs per host:	> 1	1
Stage of host:	Late 2nd. nymphal or young adult.	Early 2nd. nymphal stage.
Sex of host:	Female.	Male and female.
Size of larva & adult:	Smaller.	Larger.
Colour of adult:	Lighter.	Darker.
Superparasitism:	Common.	Absent.
Non-fatal concurrence with <i>C. taxi</i> :	Common.	Absent.

## ANATOMY OF PRE-IMAGINAL STAGES<sup>2</sup>

The anatomy of the egg and the pupa is gross while that of the larva is done in greater details.

### EGG

The colourless egg (Fig. 1) is cylindrical and 0.1052 mm. long. It is pedicellate with the pedicel so short that it can not be felt on the outer surface of host's dorsum. The pedicel functions as suspensorium to suspend the egg in the body cavity of the host. The shape, as well as the pedicellate nature, of the egg can be taken as distinguishing characters of *M. taxi* to separate it from *Aphycus melanostomatus* (Imms, 1918), which is also recorded from Great Britain.

### FIRST INSTAR LARVA

The first instar larva (Fig. 2) is dirty white and lies free in host's body. The shape of the larva is from a flattened sphere to elongated form. The hemispherical head (h) is distinguishable from the body for its brown colour. The body region exhibits faint segmentation. The cuticle is transparent and through it the digestive system with circular midgut (mg) filled with brownish material and the nervous system can be studied. The tracheal system can be seen in the form of two lateral trunks with five ramifications but the spiracles are wanting. The fat bodies, like small opaque globules, are distributed at random. The larva is 0.126 mm. long and naked. It is haemophagous and has not yet killed the host.

### SECOND INSTAR LARVA

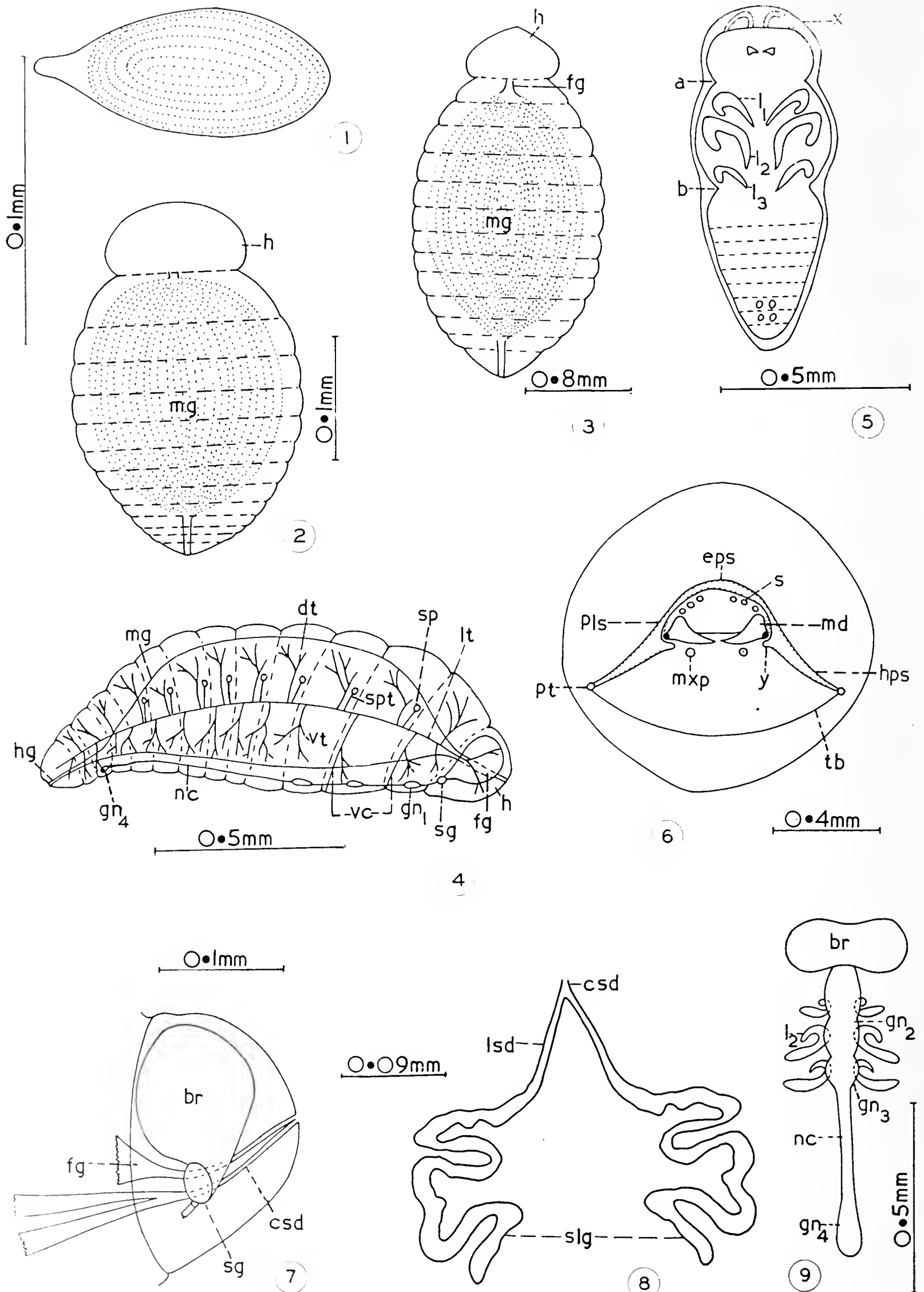
The second instar larva (Fig. 3) is clearly elongate, broadest in the middle, and with a subtriangular head (h) distinct from the body region. It is 1.037 mm. long. The segments are distinct with the 13th. segment almost narrowly rounded. The foregut (fg) and hindgut are very short but the midgut (mg) is very wide, full of dark material and extends from 1st. to 11th. segments. The tracheal system is conspicuous with lateral trunks, their ramifications and the spiracles as in the fully-grown larva. The ventral nerve cord has 4 ganglionic swellings. The first three segments have a pair of imaginal leg buds in each. The entire body region is enclosed in a thin external membranous envelope which never extends over the head.

### THIRD INSTAR LARVA

When fully-grown the larva (Fig. 4) is elongate, subcylindrical and 1.17 mm. long. It is dirty white and opaque, non-setose, broadest in the middle and gradually narrowed towards either end. The entire head (h) is dome-shaped with short narrow transverse slit-like mouth in the centre. On each side of the head rim lies an inconspicuous depression (Fig. 6, pt) comparable with the posterior tentorial pits of hymenopterous larvae (Short, 1952). These pits are connected by a semi-circular tentorial bar (tb) hanging in the lumen of the head capsule and are comparable with the tentorial bar of other hymenopterous larvae (Short, 1952). Laterally the mouth is limited by arc-like short pleurostomae (pls) whose posterior processes (y) are distinctly present. The anterior ends of the pleurostomae are joined by a semi-circular thinly sclerotised band comparable with the epistoma of hymenopterous larvae (eps). The area thus

<sup>2</sup>For more information see *Indian Journal of Entomology* 19(4), 1957.

enclosed between the epistoma and the mouth may be taken as the clypeo-labral area and bears three pairs of sensoria (s). The hypostomae (hps) are paired oblique sclerotic bands extending from the posterior tentorial pits to the respective pleurostoma. The mandibles (md) are of orange colour. These are conical in shape with long pointed straight apices. The lower angle of the mandibular base is modified into a small condyle which fits into the concavity of the pleurostoma. The maxillae and labium are not differentiated except for a pair of maxillary palps (mxp) in close proximity to the lower margin of mouth.





The intersegmental grooves are fairly deep. The first three segments are large while the remaining segments become gradually smaller. The larva is completely enclosed in a membranous envelope. A similar envelope has been recorded in the late 3rd. or 4th. larval instar of *Encyrtus infelix* (Thorpe, 1936). The larva is sarcophagous and ultimately kills its host.

#### DIGESTIVE SYSTEM

It (Figs. 4, 7) consists of the fore-, mid- and hindguts. The foregut (fg) is a short narrow tube extending from the mouth to the 1st. body segment. The midgut is very long and wide, extending from 1st. to 11th. segment, and occupies the greater part of the body cavity (Fig. 4, mg). Anteriorly it is narrow with its lumen in communication with the foregut while posteriorly it has no lumenar communication with the hindgut. The midgut can be differentiated from the other two not only on its size but also for the opacity. The hindgut (hg) is a short, narrow tube extending from midgut to the apex of the 13th. segment to open by the anus. It is devoid of any distinct diverticulum which is distinctly present in Braconid larva (Alam, 1952).

The paired salivary glands (Fig. 8, sgl) are brown and tubular. Each is convoluted and runs on the lateral wall of the midgut upto the 4th. segment. In the 1st. segment and close to the foramen magnum it leaves the gut as narrow, straight 'lateral salivary duct' (lsd). The two lateral ducts converge into the head capsule and ultimately fuse to form the 'common salivary duct' (Figs. 7, 8, csd). The latter passing in between the brain and the suboesophageal ganglion ends on the floor of the mouth.

#### EXCRETORY SYSTEM

It is represented by a pair of non-convoluted, tubular malpighian tubules of almost uniform cross-section which run on the latero-ventral face of the midgut with their free anterior ends reaching upto the 3rd. segment. The posterior ends taper and open into the ventral wall of the hindgut near its junction with the midgut.

#### RESPIRATORY SYSTEM

The respiratory system (Fig. 4) consists of a pair of lateral trunks (lt) which run longitudinally along the body wall from segments 1-12. Anteriorly each trunk extends into the head capsule to end by two branches. Posteriorly, it enters the 13th. segment and bifurcates there. Eight pairs of spiracles (sp) are present on 2nd. to 9th. terga slightly dorsal to the lateral trunks and very close to the anterior intertergal grooves. They are connected with the lateral trunks by short vertical spiracular tubes (spt). In the spiracle-bearing segments the lateral trunks give out a pair of 'dorsal trachae' (dt) and another pair of 'ventral trachae' (vt). The dorsal trachae arise slightly posterior to the spiracular tubes and ramify on the latero-dorsal area of their respective segments. The ventral trachae are given out near the posterior intersegmental grooves. They not only supply branches to the latero-ventral area of their respective segments but also to the segment immediately posterior to them. Similarly, dorsal and ventral trachae are also given out from the lateral trunks in segments 1, 10, 11 & 12. The ventral trachae of one side in segments 1 & 2 meet their counterparts of the other side to form the two ventral commissures (vc). The respiratory system as such on comparison with that of *Stenobracon deesae* (Alam, 1952) appears to be better evolved.

← Fig. 1, egg. Fig. 2, dorsal view of first instar larva. Fig. 3, dorsal view of second instar larva. Fig. 4, lateral view of third instar larva. Fig. 5, ventral view of pre-pupa. Fig. 6, facial view of head capsule. Fig. 7, lateral view of head capsule. Fig. 8, salivary glands. Fig. 9, nervous system. Abbreviations: a, constriction between head and 1st. body segment; b, constriction between 4th. and 5th. body segments; br, brain; csd, common salivary duct; dt, dorsal trachea; eps, epistoma; fg, foregut; gn<sub>1-4</sub>, 1st. to 4th. ganglionic swellings; h, head; hg, hindgut; hps, hypostoma; lsd, lateral salivary duct; lt, lateral trunk; md, mandible; mg, midgut; mxp, maxillary palp; nc, nerve cord; pls, pleurostoma; pt, posterior tentorial pit, s, sensory papilla; sg, suboesophageal ganglion, slg, salivary glands; sp, spiracle; spt, spiracular tube; tb, tentorial bar; vc, ventral commissure; vt, ventral trachea; x, moult of fully-grown larva; y, posterior process of pleurostoma; fig. 11-3, thoracic leg buds.



## NERVOUS SYSTEM

The brain (Fig. 9) is distinctly bilobed and occupies almost the entire head capsule (br). It is connected with the suboesophageal ganglion (Figs. 4, 7, sg) by a pair of circumpharyngeal connectives. The suboesophageal ganglion is very small. The ventral nerve cord (Figs. 4, 7, nc) extends from the suboesophageal ganglion to the 11th. segment. In the first three segments it develops three ganglionic swellings ( $gn_{1-3}$ ) with definite constrictions between them and flanked by respective paired leg buds (Fig. 9, 1<sub>2</sub>). The remaining portion of the nerve cord is narrow with the posterior end swollen to form its fourth ganglion ( $gn_4$ ). This system on the whole appears to stand on a higher evolutionary level when compared with that of a braconid (Alam, 1952).

## PUPAL STAGE

A pre-pupal stage intervenes between larval and pupal stages. It appears within the last larval coat (Fig. 5, x) and develops two distinct constrictions—one between head and 1st. segment and the other between 4th. and 5th. segments (Fig. 5, a, b). Besides, the pre-imaginal buds of various appendages evert out as undifferentiated rudiments ( $1_{1-3}$ ). The pre-pupa transforms into a typical hymenopterous pupa. It is colourless in the first instance, but soon takes up the colour of the adult. No typical hymenopterous cocoon is constructed—a confirmation of similar finding in *Aphytis diaspidis* (Alam, 1956) and in *Thomsonisca brittanica* (Alam, unpublished).

## LIGHT EXPERIMENTS ON ADULT PARASITE

Three different types of experiments were set up to study photokinetic and phototactic behaviour. All experiments were carried out in a constant temperature room running at 27°C with 70% relative humidity, and the parasites selected were kept in the dark room for 12 hrs.

### EXPERIMENTS ON PHOTOKINESIS

The apparatus consisted of a platform with an intense light electric lamp at its top. The tube of the lamp was turned perpendicular to the graph paper which was kept at a distance of 51.5 cm. below it. The aperture of the diaphragm was adjusted to different diameters. An enclosure with black walls with graph paper within it was placed below the lamp. The intensity of the light was controlled by a transformer and also by altering the aperture of the diaphragm. The light was diffused by using filters. The low and high light intensities for the experiments were 0.0316 and 1.59 log ft. lamberts respectively. The duration of each experiment was seven minutes during which the movements of the tiny parasites on the graph paper was traced and their behaviour recorded.

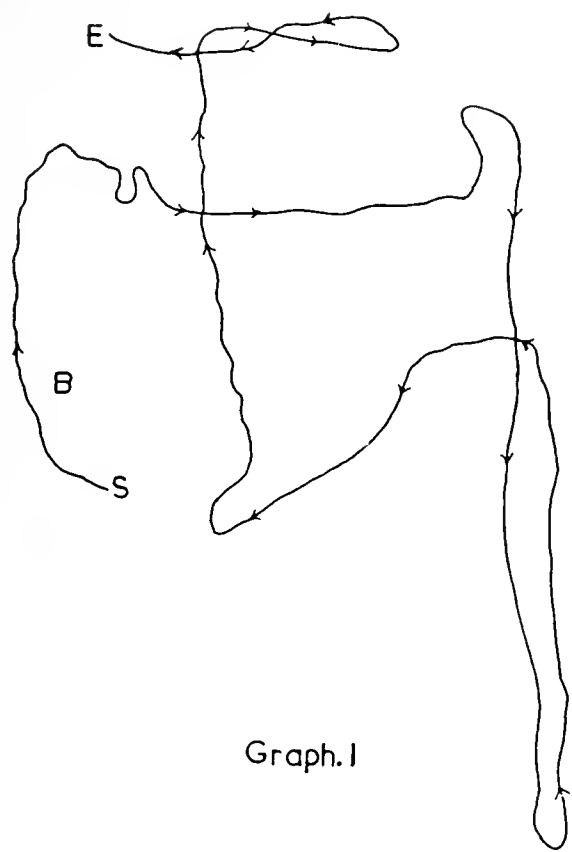
Insects in turn were subjected to low and high lights. Seventy-five percent of the insects spent more time moving at the lower light intensity; but the speed (orthokinesis) of all the insects was greater in greater illumination (speed at lower light = 0.31 cm. per second; speed at higher light = 0.47 cm. per second). All that can be deduced is that whereas the higher light intensity appears to have a depressing effect on total period of activity, orthokinesis is simultaneously increased by it (Graph 1A, B).

### EXPERIMENTS ON PHOTOTAXIS WITH ONE SOURCE OF LIGHT

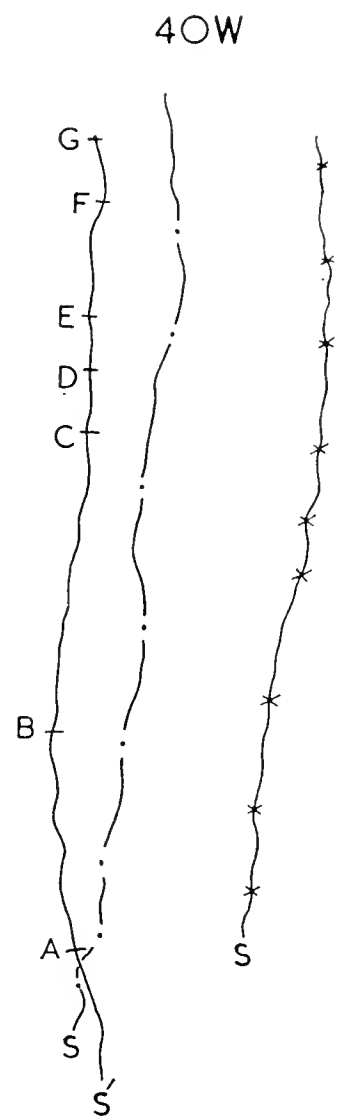
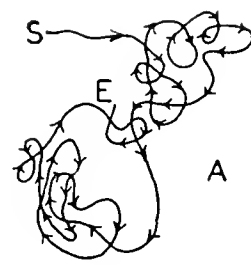
A rectangular wooden box, 45.5 × 23 cm., was blackened inside and a rectangular hole 8.5 cm. wide was made in the middle of one of the smaller sides, while the other smaller side was totally removed. The hole was closed with a glass beaker, 16 × 7.5 cm., full of cold water and a 40 W Mazda milky bulb was hung behind the beaker as a source of light. The floor of the box was covered with graph paper. The parasite was released on the graph paper at a distance of 39.5 cm. from the source. The course of its movements was traced. Halts made by the parasite were marked and distances between successive halts were measured. The intensity of the source at each halt was

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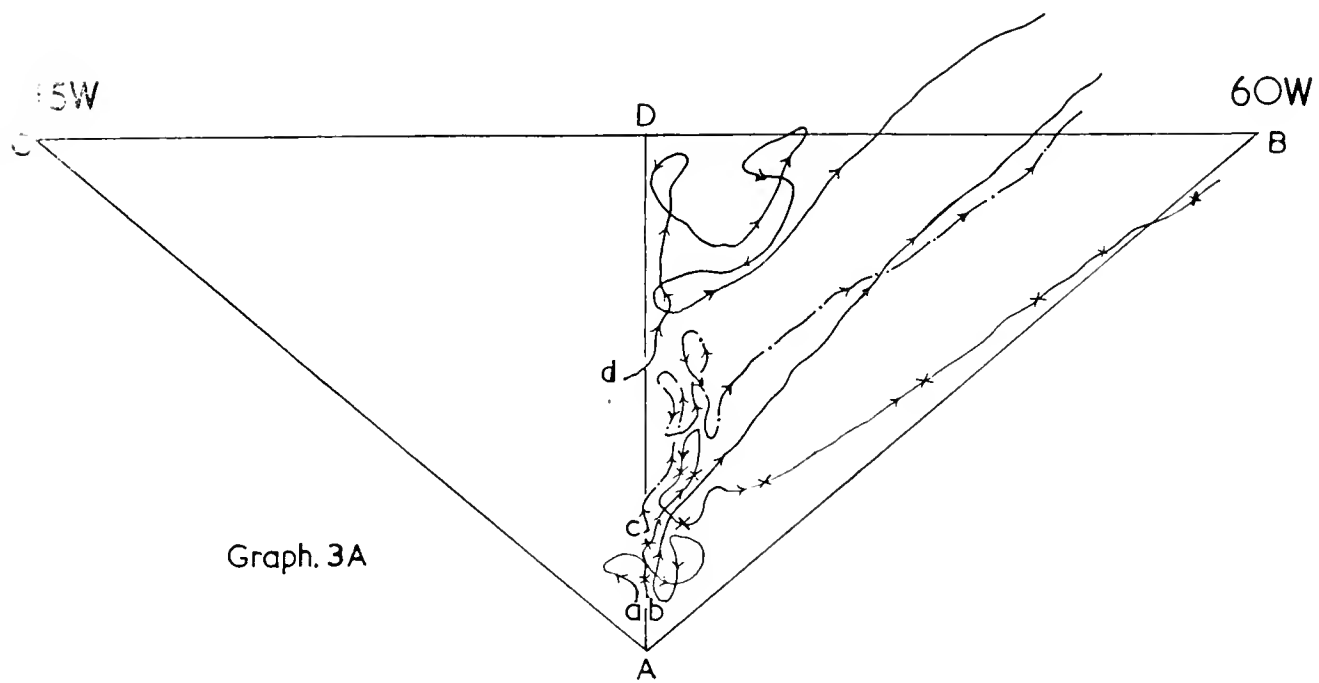
Graphs 1-3. Course of movement of parasite in experiments of photokinesis. Graph 1A, low light. Graph 1B, high light. Graph 2, one source of light. Graph 3A, two unequal sources of light. Graph 3B, two equal sources of light.



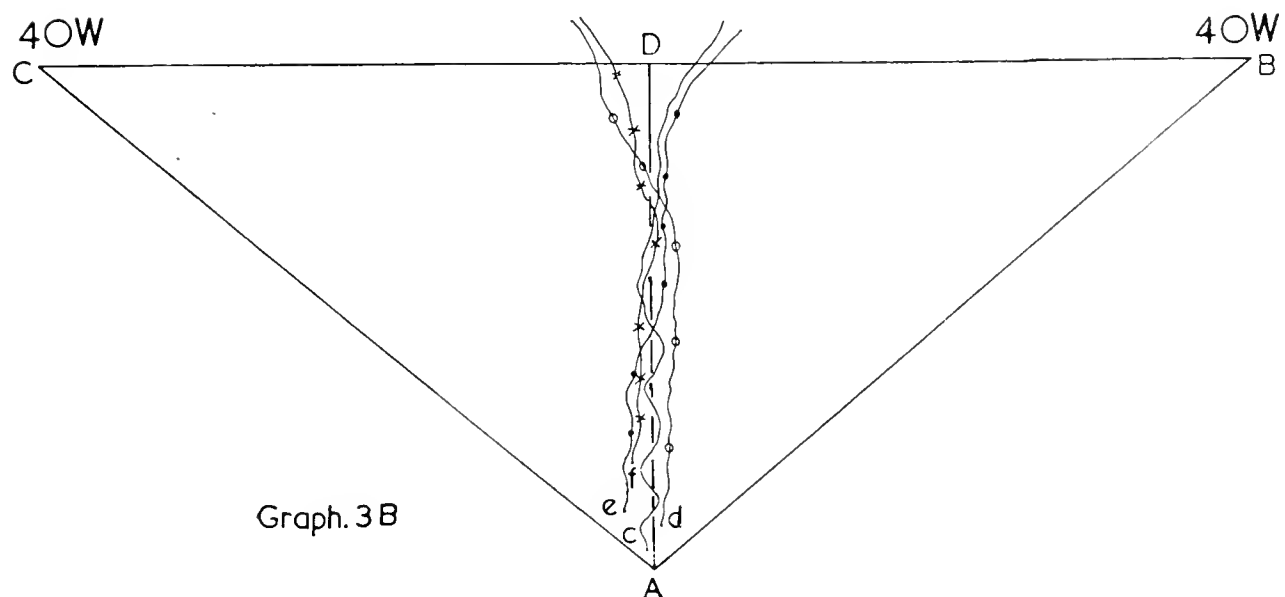
Graph. 1



Graph. 2



Graph. 3A



Graph. 3B

recorded with the help of Weston Photometer while a stop watch was used to record the times between successive halts.

All insects, without exception, when released, moved in an almost straight line towards the source of light, their speed tending to increase (0.4 cm., 0.78 cm., 1.9 cm. per second at light intensities of 50, 90, and 200 ft. candles respectively) as they approached the electric bulb (Graph 2).

#### EXPERIMENTS WITH PHOTOTAXIS WITH TWO LIGHT SOURCES

A rectangular box,  $45.5 \times 23$  cm., was blackened inside. One of the larger walls was movable to facilitate observation. In the side opposite to the movable side a 60 W Mazda milky bulb was hung while in another corner a 15 W Mazda milky bulb was hung at the same height—in case of two equal sources both bulbs were 40 W. An isoscelles triangle, ABC, was drawn on graph paper and the base of the triangle was bisected by a perpendicular line, AD, from the vertex. The graph paper was so placed in the box that the basal angles came exactly underneath the bulbs.

The intensities of the two unequal sources of light at the releasing points 'a, b, c, d' were 30 and 135, 30 and 135, 35 and 165, 40 and 155 ft. candles respectively. In this experiment all insects moved towards the higher source of light, disregarding the lower one (Graph 3A). These insects were, probably, exhibiting a telotactic reaction to light.

When two sources of equal light intensity (40 W) were used, all insects released on points 'c, d, e, f' moved along the bisecting line, AD, between them indicating positive photo-tropotaxis (Graph 3B).

The fact that in the photokinetic experiments *M. taxi* moves at a greater speed in light of higher intensity is, probably, associated with the higher percentage of parasitism occurring in better illuminated regions of the yew tree at Silwood Park as referred earlier. The reaction of the parasite in experiments on phototaxis with one source of light where activity of the parasite was accelerated with the increasing light might lead to the same conclusion.

#### HOST SELECTION

Three type of experiments were done in a constant temperature room (temp.  $27^{\circ}\text{C}$ ., R.H. 70%) to study host selection behaviour of *M. taxi*. In the first experiment a rectangle,  $2 \times 1\frac{1}{2}$  cm., was drawn in the middle of a piece of bristol board,  $7 \times 1\frac{3}{4}$  cm. This rectangle was further divided into 12 equal squares, each measuring  $0.5 \times 0.5$  cm. These were equally distributed into three longitudinal rows. The 1st. longitudinal row had unparasitized and parasitized *E. taxi* alternating with each other, the middle row had unparasitized coccids only. Similarly, the last row had parasitized coccids. The coccids selected were not removed from the leaves of the host plant but a small piece bearing a scale was cut out from the leaf and glued to each square. The parasitized coccids used were parasitized in the previous 24 hrs. The bristol board with coccids arranged in rows was put in a specimen tube,  $8 \times 2$  cm. The latter was wrapped in black paper except above the area with squares. In these conditions the parasite mostly remained in the uncovered part of the tube. The female parasite which had already mated and had laid a few eggs prior to her release was watched through a binocular microscope.

On release the parasites were observed many times visiting from unparasitized to parasitized coccids and vice versa (visits to parasitized hosts = 63; visits to unparasitized hosts = 67). They laid eggs on unparasitized coccids, then on parasitized coccids and after some time in a reverse sequence and so on (oviposition in parasitized and unparasitized hosts are 7 and 8 respectively).

The second experiment had *E. taxi* containing pupae of the parasite in the 1st. row. The middle row and the 3rd. row had unparasitized hosts and hosts with fully-grown larvae of the parasite respectively. The parasites when released never stayed on parasitized hosts after making a survey of the latter by tapping with the antennae. They had always laid eggs in unparasitized coccids (32 times). There were very few cases in which the ovipositor penetrated the dermis of parasitized host (twice in hosts with larvae and only once in host with pupa), and then it was immediately and quickly

withdrawn giving the impression that she could detect the presence of some foreign body in the host.

The third experiment consisted of placing at random in the squares unparasitized coccids, coccids having fully-grown larvae of the parasite, and coccids containing pupae. This experiment was set up to see if the linear arrangement of one type of host — as in the second experiment — can influence the behaviour of the parasite. The results showed no difference of behaviour of the parasite in the two experiments. So, it is, probably, the stage of the parasite within the host that determines her behaviour.

Keeping in view the results it can be said that *M. taxi* fails to differentiate between unparasitized hosts and hosts parasitized within past 24 hrs. Further, she is also found to differentiate well between unparasitized hosts and hosts with advanced developmental stages of the parasite irrespective of the type of arrangement of hosts. Such host selection behaviour seems analogous to the 'graded oviposition response' of *Ooencyrtus kuvanae* (Lloyd, 1938) and may also be taken as probable explanation for the prevalence of super and multi-parasitism in the field.

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# The Seasonal Activity and Oviposition Behaviour of Two Parasites of the Diamondback Moth, *Plutella maculipennis* (Curt.) (Tineidae: Lepidoptera)

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## ABSTRACT

The diamondback moth, *Plutella maculipennis* (Curt.), is an important pest of cabbage in Australia, where it was accidentally introduced from Europe. Lloyd (1940. Proc. Royal Soc. B. 128: 451-89) searched for its natural enemies in England and Europe. After studying their natural incidence of attack and oviposition behaviour he selected two ichneumonids, *Diadromus collaris* Grav. and *Angitia* (Horogenes) *cero-phaga* Grav., which appeared to have very little competition with each other. Subsequently, they were released in Australia. Both the parasites established there quite successfully. Rough estimates in different seasons in the fields around Adelaide, South Australia, showed that during the summer of 1951-52 up to 40 per cent of the host pupae were parasitized by the former species and up to 80 per cent by the latter. *Angitia* was predominant in the spring and early summer whereas *Diadromus* reached its peak of activity later in the summer. It was found that the optimum rearing temperature in the laboratory for *Angitia* was lower than that for *Diadromus*. That explained the two distinct peaks of activity for the parasites in the field.

The oviposition behaviour of *Diadromus* was studied in the laboratory under controlled environmental conditions to see what factors influenced it. Female parasites were kept separate each with a fertile male at 18° and 25° C, and they were offered four or eight host pupae per day for laying eggs. Temperature produced significant influence on the longevity and fecundity of the parasites. On an average, a female laid 96.5 eggs and lived for 26 days at 18° C. and laid 75 eggs and lived for 16.5 days at 25° C. (published elsewhere). When the average number of eggs laid per female per day were plotted against the days of life the curve showed a second peak. It was possibly due to the fact that the females which died sooner than the others were also the ones which laid a smaller number of eggs, and thus the average showed a second peak.

To find out whether a female distributed its eggs selectively or at random it was tested from the data on egg-laying if the number of hosts parasitized was independent of the number of eggs laid per day. The significant chi-square showed that in case of four host pupae per day egg-laying was selective rather than at random.



# Biological Control Methods (Rearing and Shipping Methods)

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According to the method of work used at the European Laboratory of the CIBC, each new biological control problem against a certain pest requires a period of preliminary research, which takes more or less time in proportion to the subject. During this period, the abiotic and biotic factors constituting the environmental resistance are focussed; if the biotic factors, especially parasites and predators, are important, then mass rearing and shipping methods must be accurately studied. For any Entomologist chiefly accustomed to scientific researches, these two practical phases of biological control offer the less interesting side of the problem and are often overlooked. For a fieldstation, such as ours is, responsible for the mass exportation of entomophagous insects, these two final stages of a particular work are on the contrary of great consequence. Through this study we want to know and to realize the most suitable environmental conditions in order to achieve the least possible mortality. If we succeed in sending to Australia from Central Italy a shipment of *Apanteles plutellae* Kurdj. with 0% mortality (as in 1951) we, with justification, feel rather pleased, especially having worked month after month at Laboratory rearings, on a subject having no scientific interest.

The mass rearing problem does not present great difficulties when dealing with species (parasites or predators) which have a relatively short preimaginal development. As a first example let us present the rearing method of two predators of *Adelges piceae* Ratz. (Hem., Adelgidae): *Pullus impexus* Muls. and *Aphidecta oblitterata* L. (of which we sent to Canada over 50,000 specimens), and that of *Apanteles plutellae* Kurdj., parasite of *Plutella maculipennis* Curt. *P. impexus* has two parasites, *Centistes scymni* Ferr. attacking the adults and *Metastenus mesnili* Ferr. attacking the pupae. For this reason the shipping of pupae or adults collected in the field is avoided and we proceed to mass rearing, collecting at first the adult larvae which show a tendency — shortly before pupation — to migrate towards the base of the infested trunks of *Abies alba* and hide under the corrugated cardboard which has been applied to them. The pupae are taken to the laboratory and confined in rearing tubes 20 cm. long and 4 cm. in diameter, through which flows a moist air current. Such rearing methods have proved excellent and no mortality has been recorded. The small cardboard box in each rearing tube may keep up to 500 *Pullus* pupae; at emergence the adults are drawn off by means of an aspirator and shut into shipping boxes. If water condensation is observed in the rearing tubes, we turn off the water tap upon the vase and pass dry air through the rearing tube. There is practically no fungal formation. It is generally necessary to alternate the dry and moist air currents. As to the mass rearing of *Aphidecta*, the problem presents different difficulties, since it is a rather rare species in our woods. The pupae being formed on the trunk are rather heavily attacked by a phorid, *Phalacrotophora berolinensis* Schm., and only a scanty part of the collected material is of use. In the years when the *Aphidecta* abundance was relatively high, we collected the third and fourth larval stage and confined them in cages (Fig. 1) on the infested trees. This rearing method in the field has been adopted because of the great voracity of the adult larvae. If the density of the *Aphidecta* population becomes too high or if food is wanting, we may observe in the cages a certain amount of cannibalism. In one metre high cage there is room for some 300 adult larvae. Care is taken to put into the cage larvae of the same age, so that we may take out all pupae at the same time. In the laboratory the pupae are reared using the same system as with *Pullus*. The setting of a cage on the tree takes, with some practise, about an hour. The same system of cages has been employed for different experiments on *A. piceae*, for the finest nylon prevents the entrance of parasites and predators. The *A. plutellae* rearing was undertaken from the economic point of view because of the season (Mediterranean summer), we used boxes containing moist salt, which were supplied with a strip of nylon fabric, covered with an overturned Petri dish. We know exactly the duration of the *Apanteles*

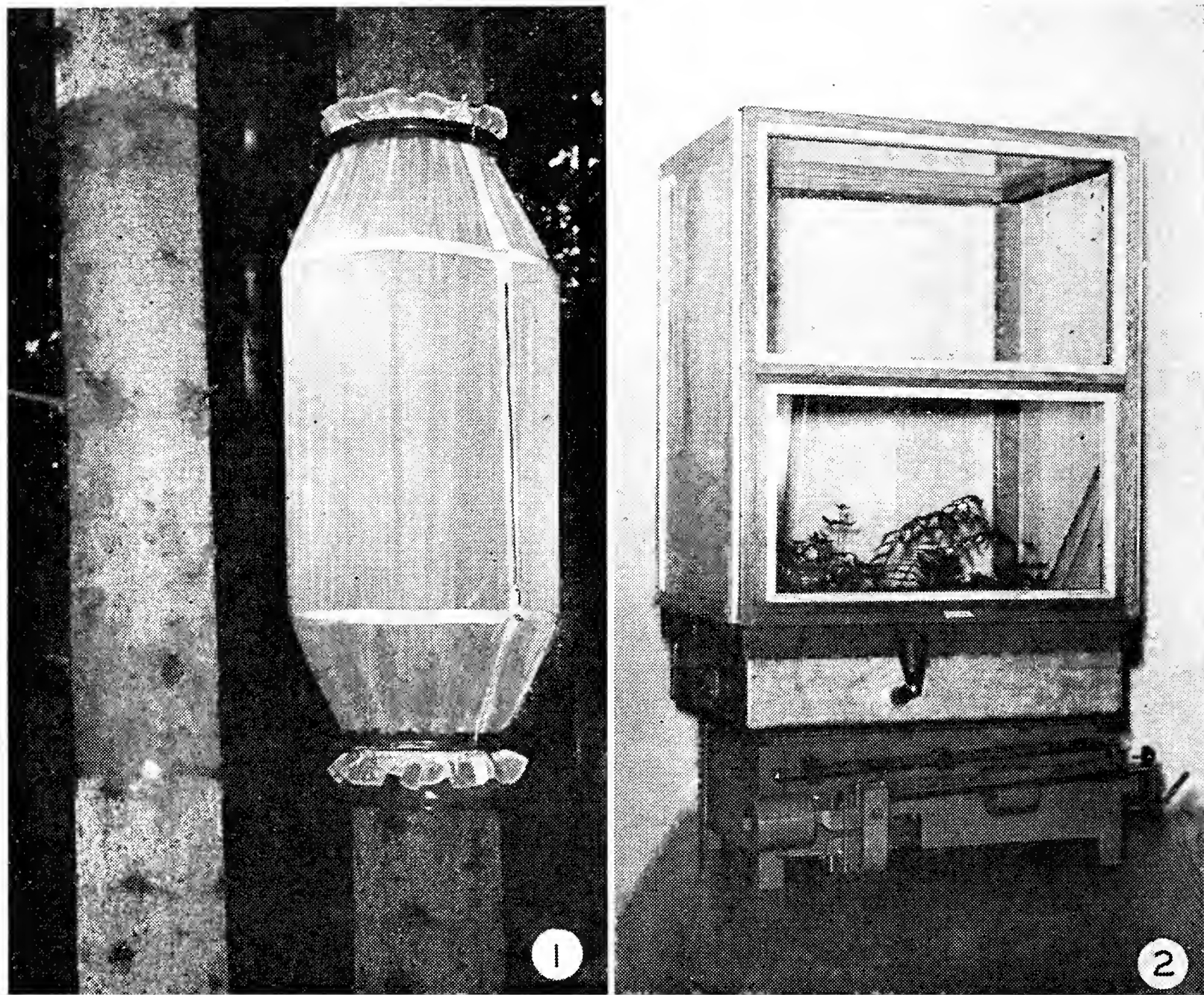
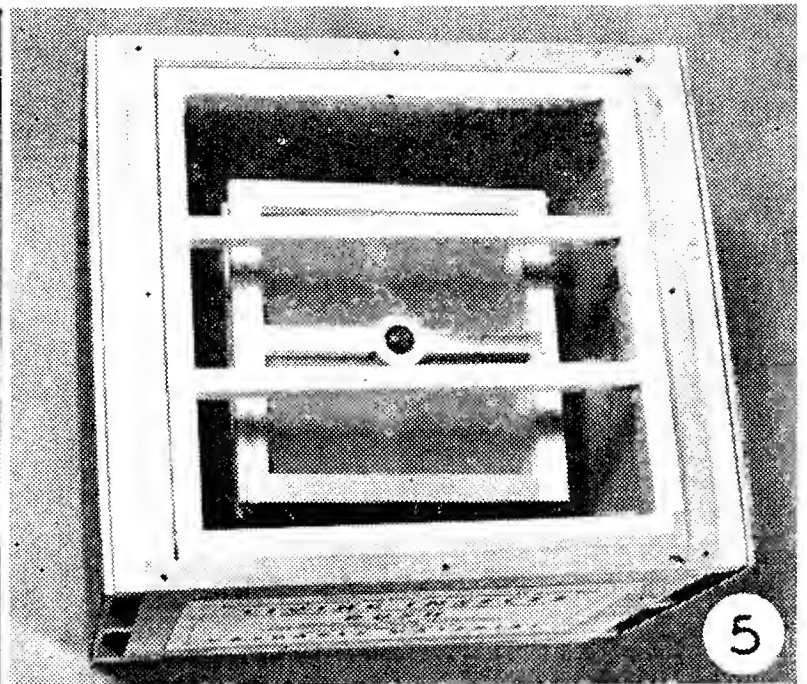
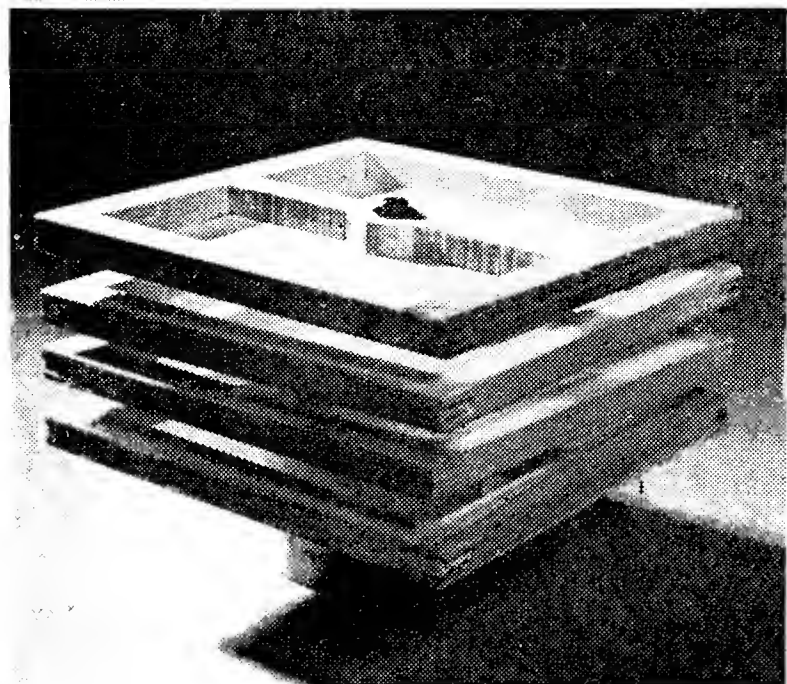
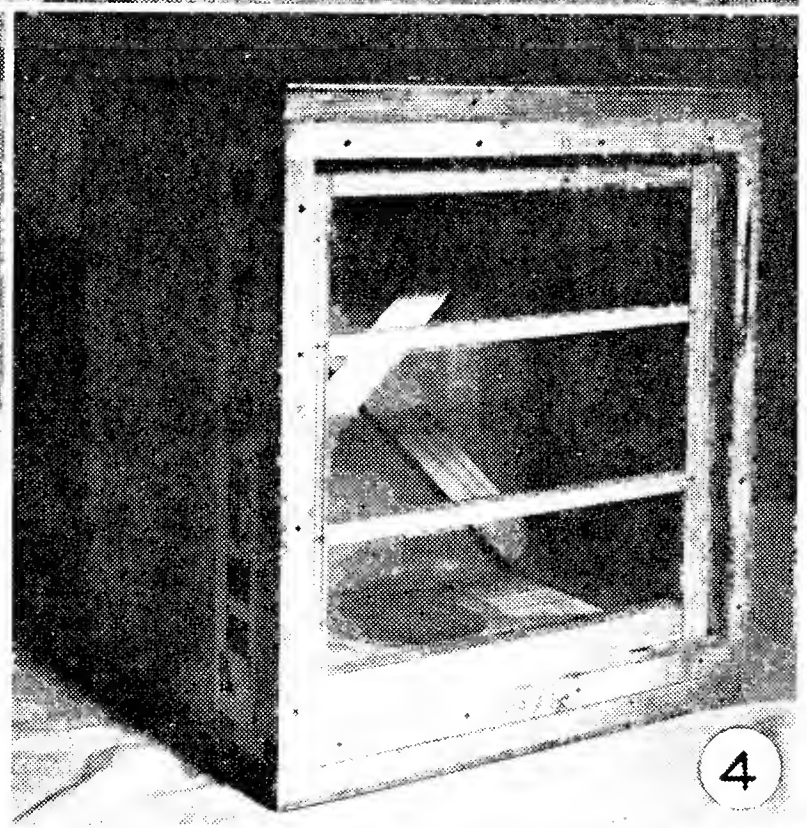
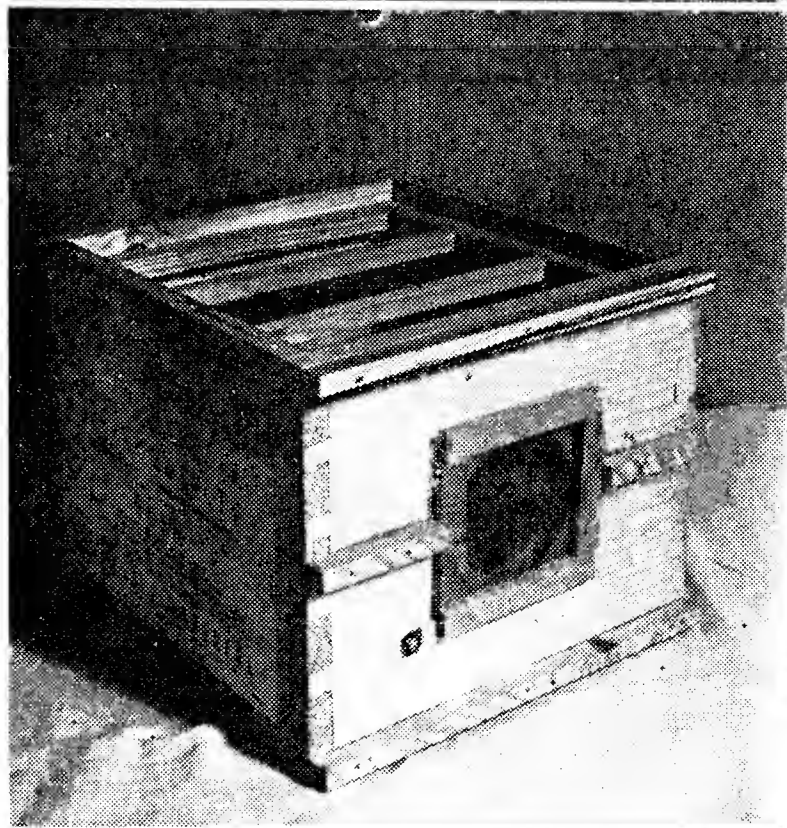
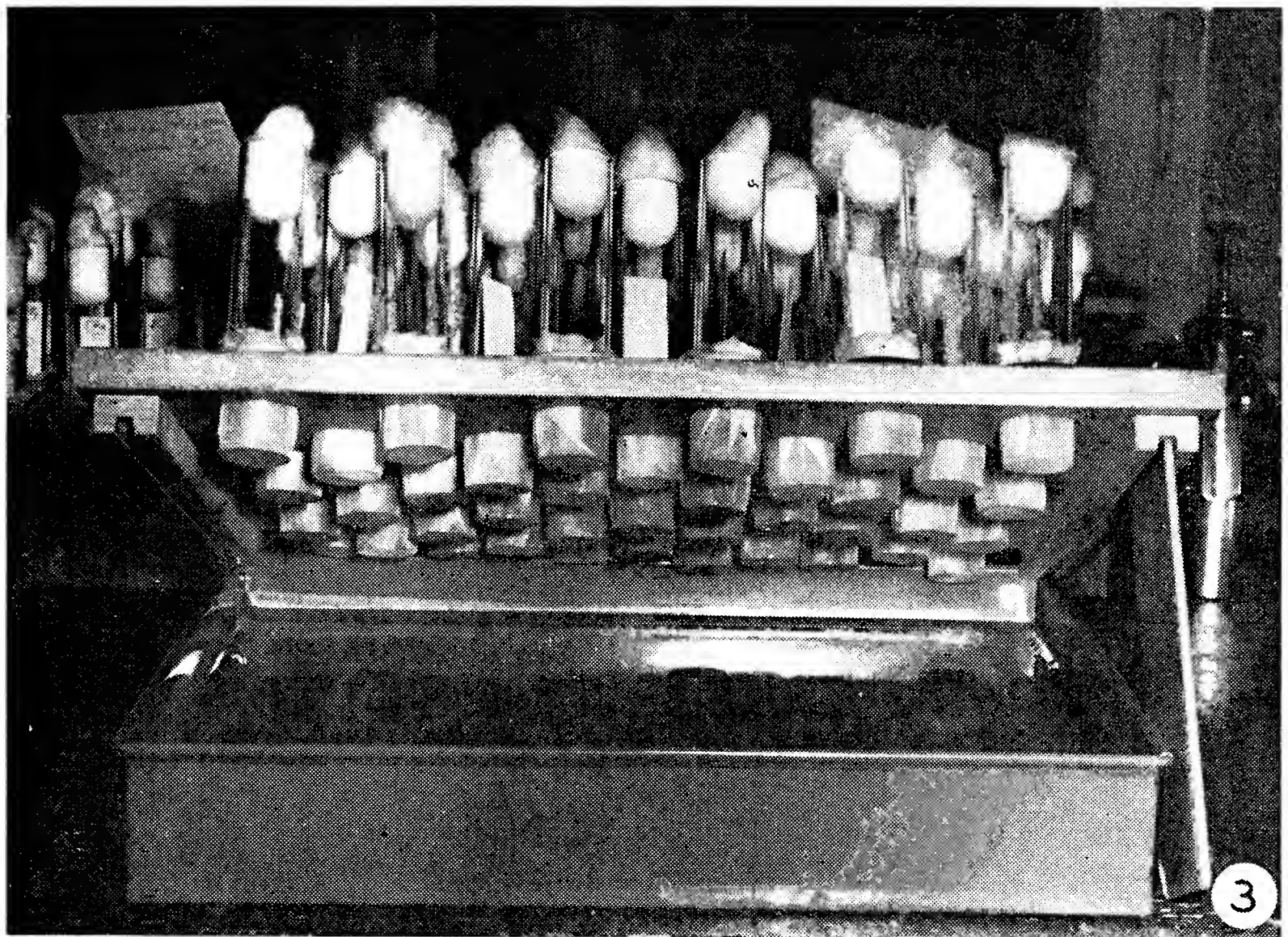


Fig. 1. *Abies alba* trunk infested by *Adelges piceae* Ratz. (left) with the rearing cage (right) for *Aphidecta obliterata* L. Fig. 2. Rearing method for hibernating parasites.

larval stage in its host, and the parasitized *Plutella* larvae were confined — 24 hours before the *Apanteles* larvae left their hosts — in small organdy or nylon sacks containing food (cabbage) and suspended above a large water tray. In this way the *Apanteles* larvae spun their cocoon on the walls of the small sack; the wall portion with the cocoon was cut out and stitched on cardboard; the cardboard with 150-200 cocoons was nailed on the interior walls of the shipping box.

The mass rearing problem becomes particularly complicated when an aestivation or an hibernation period exists. The stay of an insect at a certain stage at non optimal conditions may compromise the entire laboratory work. As an example of this we shall mention the two following instances: the rearing of parasites of *Cheimatobia brumata* L. and parasites of leaf-miners. The adult *Cheimatobia* larvae, parasitized or not, are confined in rearing cages (Fig. 2) having two nylon changeable walls and two of glass, with an anterior door. This bottomless cage fits exactly on to a metal tray which is provided with a funnel on each of the fore- and rearsides, through which we introduce water equivalent to that lost by evaporation; this occurs at a certain rate, measured by a balance lying lower. To the tray may be applied a tube to let in an air current at environmental temperature, in order to avoid fungus formation. The milieu in which the host pupae and the parasite pupae spend their hibernation period is composed of a rather porous layer on the bottom of the tray and of a superficial earth layer. In the place of the latter we may put a mixture of sand and sterilized sawdust. We used a very economical method for the rearing of leaf-miner parasites, in particular parasites of *Lithocolletis* species. This method (Fig. 3) permits a regular rearing during the







diapause period. The tray contains pure water; the lower opening of each rearing tube is covered with nylon or organdy, the upper one with cotton. In this case, the only cause of mortality during the winter is due to the mites which happen to be shut into the tube. There is no fungus formation. This method has proved very convenient, especially for the study of hyperparasites hibernating in the last larval stage.

A very important factor at the conclusion of any work of biological control in our station is the preparation of the shipping material. Not long ago, the material collected in the field was shipped with parasites and hyperparasites by sea and there was a very high mortality. At that time, as a rule, the material underwent an elaboration at the receiving station; today, if the material and funds allow, we try to supply the end station with entomophagous material ready to be set free in the field, free of secondary parasites and possibly of diseases. With an increase in air mail facilities we succeed very often in shipping material in an adult stage, which can be immediately liberated. For this purpose we use a shipping box, manufactured in different sizes, capable of being changed inside in accordance with the shipped insect. The Fig. 4 represents a simply-built box, such as is used for the shipping of Coleoptera predators (as *Pullus* or *Aphidecta*) to America; it is provided at the bottom with a moist and sterilized moss layer (*sphagnum*) and with two openings at the opposite walls for the passage of air. On the walls with no openings we fix the cardboard with drops of agar-agar/sugar/honey composed according to the Parker formula (1948). The inside of the box reserved for the insect (adults in this case) is covered with a sheet of cellophane on the upper part, for the customs inspection or for the immediate examination in the laboratory. For the shipping of adult Diptera (as *Cremifania*, *Syrphus* etc.), care is taken to fix on to the middle of the box a wet sponge, protected on the outside with blotting paper. For the shipping of material parasitized in the laboratory or of pupae the emergence of which is expected during the trip, two possibilities are provided: the first was used to ship, to New Zealand, parasites of *Coleophora frischella* L. with emergence of the chalcids en route; the *Coleophora* material is arranged between the cellophane sheet and wire-netting fixed to the underpart of the frame, and the parasite adults can find food and room for flying in the space below. The second (Fig. 5) was used for pupae of midges (*Aphidoletes thompsoni* Moehn) or for parasitized eggs of *Nezara viridula* L. and *Pieris rapae* L. etc.; the lower side of each frame is covered with nylon, the upper with netting with narrow meshes which allows the emergence of the predators or parasites. We shall not give here the mortality percentages registered in these overseas shippings, which are very low and already published in particular studies. The shipping system is generally based on preliminary researches, which determine the mortality rate.

This conclusive phase of the work in biological control takes for granted that the laboratory, to which the material is forwarded, possesses the systematic and biological information about the species. Information is drawn out in a report (when preliminary researches have been made) in order to permit the identification, in the laboratory as well as in nature, of the introduced species.

# Field and Greenhouse Studies Regarding the Sources and Nature of Sorghum Resistance to the Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch)

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## ABSTRACT<sup>1</sup>

The purpose of the study was to find sources and study the nature of resistance in sorghum varieties to the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (= *Aphis maidis*).

Tests were made on 460 varieties of sorghum involving 11,922 plants. These 460 varieties included the world germ plasm of sorghum as available in the United States. Records were taken on total of 595 selections and hybrids, involving 13,662 plants.

The mechanisms of preference and antibiosis were the factors most measured. The following five measurements were employed to evaluate these two factors: per cent infestation, progeny per infested plant, winged aphids per plant day, index number, and total progeny produced by a given number of aphids confined on a plant.

It was found that Sudan type sorghums, consistently and without exception, demonstrated a high level of resistance to the corn leaf aphid in all preference and antibiotic tests. It appears that Sudan type sorghums in general carry both the non-preference and antibiotic factors for resistance.

The majority of combine-type sorghums were found to be either intermediate or highly susceptible to the corn leaf aphid.

Kafir-type sorghum was predominantly intermediate in regard to susceptibility to the corn leaf aphid.

The majority of the Sumac strains exhibited resistance to *Rhopalosiphum maidis* in the form of non-preference.

The majority of Milo type sorghums tested showed an intermediate level of resistance to the corn leaf aphid.

<sup>1</sup>For complete text see Kansas State College Agric. Exp. Sta., Tech. Bul. 82:38 pp. 1956.



# Effect of Superparasitism on Reproduction of *Trichogramma japonicum* Ashmead

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## ABSTRACT

The egg parasite, *Trichogramma japonicum* Ashmead, is one of the important natural enemies of the rice stem borer, *Chilo suppressalis* Walker. In many cases, a field parasitization of 50% or more has been recorded.

The number of hosts parasitized in a fixed population of hosts increased rapidly with initial increase in the number of parasite eggs deposited. With further increase in parasites the parasitism increased more slowly. With the increase of parasitism, the percentage of simple parasitism reached the maximum and then decreased, whereas that of superparasitism increased steadily. The maximum simple parasitism was 58.2%, and happened at a parasitism of 83.5%.

As the density of parasites in a fixed population of hosts increased, more and more superparasitism occurred, resulting in the following effects on the parasites:

- (1) Reduction of the mean body length of the emergents.
- (2) Steady decrease of the emergence rate of parasites.
- (3) Decrease of the female proportion of the emergents, because of the domination of males over females when in competition with one another.
- (4) Remarkable decrease of the average number of eggs laid by a female parasite.
- (5) Imperfect development of some of the emergents.

Therefore, there is an optimum parasitism for maximum reproduction of the next generation of *Trichogramma*. The estimated optimum parasitism is of about 84%.

The egg parasite, *Trichogramma japonicum* Ashmead, is one of the most important natural enemies of the rice stem borer, *Chilo suppressalis* Walker, in Japan. In many cases, a field parasitization of 50% or more has been observed. To obtain a higher degree of control over the rice stem borer, a large number of the egg parasites were

TABLE I — Relation Between Number of Parasites and Rate of Parasitism.

Number of parasites per 100 hosts	Parasitism %	Monoparasitism %	Polyparasitism %
10	8.2	7.7	0.5
20	18.4	16.3	2.1
30	26.9	22.5	4.4
40	33.9	26.9	7.0
50	39.8	30.0	9.8
60	44.8	32.3	12.5
70	56.0	40.7	15.3
80	65.3	47.4	17.9
90	72.9	52.5	20.4
100	78.9	56.0	22.9
110	83.5	58.2	25.3
120	87.2	55.6	31.6
130	90.0	51.3	38.7
140	92.2	46.6	45.6
150	93.9	41.7	52.2
160	95.2	36.9	58.3
180	97.0	28.2	68.8
200	98.1	21.0	77.1
220	98.8	15.4	83.4
240	99.1	11.1	88.0

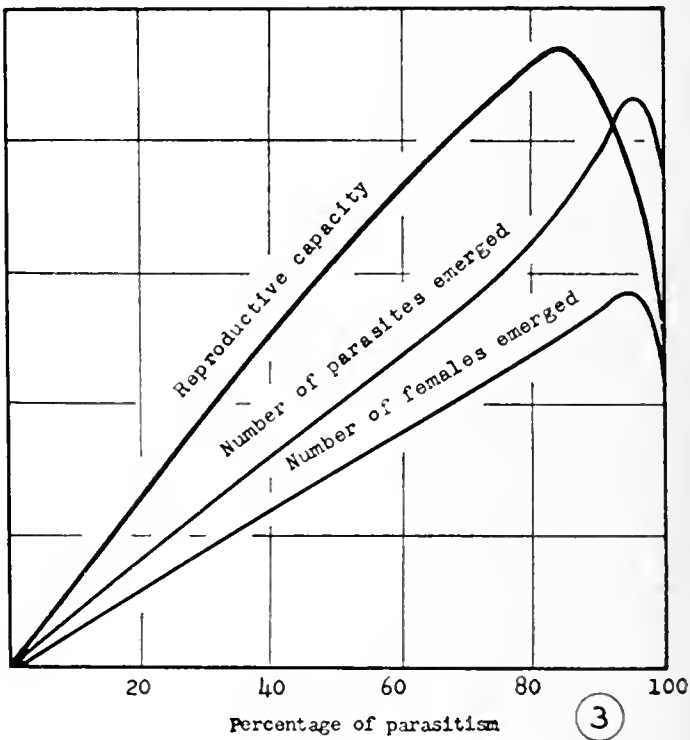
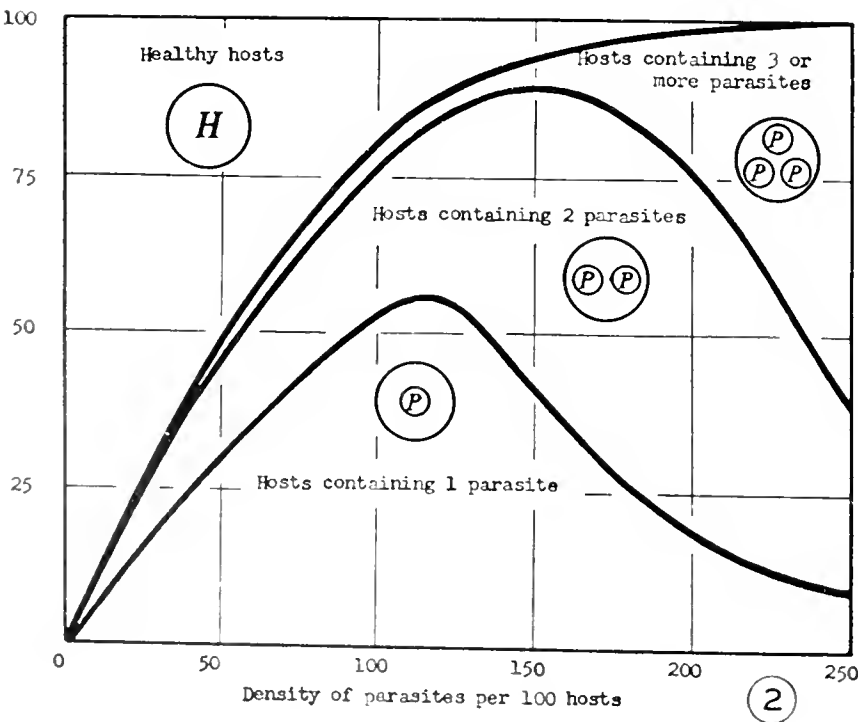
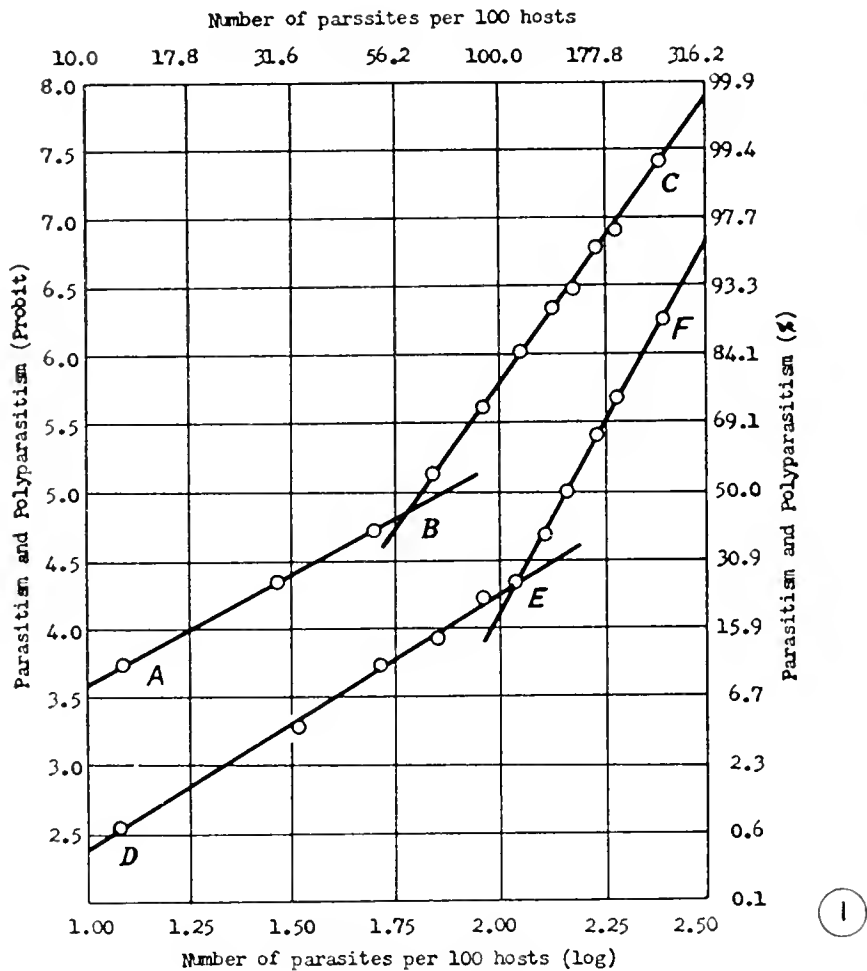
bred on the eggs of *Ephestia cautella* Walker and liberations of the parasites were attempted, but the results were not so successful. To modify a condition of equilibrium already highly adjusted, it was necessary to liberate an enormous number of parasites. Oftentimes adverse results were obtained because reproduction of the following generation of the parasite was reduced by effects of superparasitism.

The number of hosts parasitized in a fixed population of hosts increased rapidly with initial increase in the number of parasite eggs deposited. With further increase in the number of parasites, the parasitism increased more slowly, because a given host was attacked more than once by one or more parasites.

With the increase of parasitism, the percentage of monoparasitism (or single parasitism) reached the maximum and then decreased, whereas that of polyparasitism (or superparasitism) increased steadily. The maximum monoparasitism was 58.2%, and it was found at a parasitism of 83.5% (Fig. 2).

Relation between parasitism and the number of parasite eggs deposited in 100 hosts can be represented by the following formulas,

$$Y = 1.6138X + 2.0001 \dots\dots\dots AB$$
$$Y = 4.2073X - 2.6122 \dots\dots\dots BC$$





where X is number of parasite eggs deposited in 100 hosts in common logarithm, and Y is parasitism in probit. In a similar way, relation between polyparasitism and the number of parasite eggs deposited in 100 hosts can be represented by the following formulas (Fig.1).

$$Y = 1.8325 + 0.5932 \dots \dots \dots DE$$
$$Y = 5.5000 - 6.9142 \dots \dots \dots EF$$

As the density of parasites in a fixed population of hosts is increased, more and more superparasitism occurs, resulting in the following effects on the parasites:—

- (1) Reduction of the mean body length of the emergents.
- (2) Steady decrease of the emergence rate of the parasites.
- (3) Decrease of the female proportion of the emergents, because of the domination of males over females when in competition with one another.
- (4) Remarkable decrease of the average number of eggs laid by a female parasite.
- (5) Reduction of the vitality of the parasites.
- (6) Imperfect development of some of the emergents, without accompanying wing expansion.

Effects of superparasitism on the reproduction of *Trichogramma* can be estimated numerically by multiplying, (A) number of parasites in a host, (B) Emergence rate, (C) female proportion, and (D) number of eggs oviposited by one female parasite.

TABLE II — Effect of Superparasitism on the Reproduction of *Trichogramma*.

Number of parasites in a host (A)	Emergence rate (B)	Female proportion (C)	Number of eggs oviposited by one female (D)	Reproductive capacity (A x B x C x D)
1	0.69	0.84	50.1	29.04
2	0.57	0.61	17.0	11.82
3	0.12	0.40	6.5	0.94

As may be seen from Fig. 3, the number of parasites emerged from a fixed population of hosts reaches the maximum at a parasitization of 95%. But their reproductive capacity attains the maximum at a parasitization of 83.5%, and then decreases remarkably at higher percentages of parasitism, owing to the above mentioned effects of superparasitism. Therefore, there is an optimum parasitism for the maximum reproduction of the next generation of *Trichogramma*. The estimate optimum parasitism is of about 84%.

The utilization of indigenous parasites involves principles somewhat different from those concerned with parasite introductions. In the latter the aim is to build up a state of natural balance, whereas, in the former, efforts are largely concerned with the modification of biotic balance already established to a high extent. So far as concerned experiments with *T. japonicum*, it might be mentioned that the effects of superparasitism should be taken into consideration, because in order to secure higher parasitization than 84%, it is necessary to maintain a permanently readjusted equilibrium against tendencies which are operating to reduce the parasite population in the forthcoming generation.

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## DISCUSSION

G. J. KERRICH. In natural conditions is the optimum parasitism often reached, more or less, or is the degree found usually much greater or less.

K. IYATOMI. In natural conditions the optimum parasitism or higher parasitism is often observed, but parasitism usually found is of about 50 per cent or so.

# The Parasitology of Singapore Mosquitoes

By MARSHALL LAIRD  
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## ABSTRACT<sup>2</sup>

*Parasites and commensals are recorded from the larvae of 20 species of mosquitoes. Collections have been made from 164 breeding places, almost half of which are being subjected to long-term ecological study. Organisms thus far identified from larvae include ectophytic bacteria (Siderocapsa, Sphaerotilus, Zoogloea) and algae (Characium, Oedogonium, Oscillatoria); ectozoic protozoans (Colacium, Epistylis, Phacus, Phalansterium, Pleuromonas, Podophrya, Pyxidium, Scyphidia, Trachelomonas, Vorticella, Zoothamnium), rotifers (Brachionus, Habrotrocha) and a cladoceran; endophytic bacteria (Spirochaeta) and fungi (Aspergillus, Coelomomyces); and endozoic protozoans (Glaucoma, Lankesteria). Besides the larval flora and fauna, fungi (Coelomomyces, and an unidentified member of the Fungi Imperfecti), Protozoa (Crithidia, Plistophora) and hydrachnid mites are listed from imagines. Aspergillus sometimes causes heavy mortality in laboratory rearing pans, and multiple infestations with bacteria (Sphaerotilus, Zoogloea) and ciliate protozoans (Epistylis, Vorticella) may kill larvae in nature. Coelomomyces cribrus Couch and Dodge is now recorded outside the U.S.A. for the first time, from a new host, Culex tritaeniorhynchus siamensis Barraud, and Coelomomyces stegomyiae Keilin is registered from Aedes albopictus Skuse. These two parasites seldom fail to kill developing mosquitoes before pupation can take place. The majority of the organisms dealt with are specifically identified, the localities and most of the host records being new, and host specificity is considered in relation to larval habitat ecology. Attention is drawn to the scarcity of certain mosquito parasites — notably Microsporidia (Protozoa) — of common occurrence in some other parts of the world, and possible biological control applications are discussed.*

## DISCUSSION

J. S. KENNEDY. Had Dr. Laird any suggestions as to why the "classical" mosquito parasites were lacking in his fauna lists?

M. LAIRD. The distribution of these pathogens is still very far from understood. There are great areas of the tropics from which as yet we have no data, and the apparent absence of certain mosquito microsporidians and nematodes from Singapore is no more surprising than the apparent absence of Coelomomyces stegomyiae from Polynesian species of Aedes (Stegomyia). It would seem well worth while to investigate this situation on a world-wide scale, and to consider introductions of suitable mosquito pathogens into areas from which they are lacking in order to expose to them populations of dangerous mosquitoes totally lacking in immunity to the organisms concerned.

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<sup>2</sup>Complete text will be submitted to Ecology.



# De la Méthode de Lutte biologique contre *Parlatoria blanchardi* dans les Oasis du Maroc

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Rabat, Maroc

En 1941, les oasis du Maroc voisines de l'Algérie ont été envahies par *Parlatoria blanchardi* (Targ.), cochenille de la famille des Diaspidinae et ennemi sérieux du palmier dattier *Phoenix dactylifera* (L.).

S'étendant de proche en proche, cette invasion a fini par revêtir, au bout de quelques années, un caractère catastrophique.

Elle produisit une diminution notable de la productivité des palmiers, et de plus, les dattes, fréquemment recouvertes de croûtes de cochenilles perdaient l'essentiel de leur valeur et devenaient impropres à la consommation humaine.

Or, le palmier dattier est la principale ressource des habitants des régions pré-désertiques sahariennes; et c'est avec raison que l'on a appelé les dattes "le pain du Sahara".

Au Maroc, les palmiers dattiers sont souvent groupés en massifs dans les vallées des rivières telles que le Ziz ou le Drâa, créant une sorte de forêt à l'ombre de laquelle les habitants font leurs cultures annuelles ou arbustives.

Les moyens de lutte chimiques ont été essayés autrefois (acide cyanhydrique, huile blanche), mais ils n'ont pas donné de résultats. Le Service de la Défense des Végétaux du Maroc a donc orienté ses recherches vers les méthodes biologiques de lutte contre cette cochenille.

Ces travaux nous ont été confiés, et à leur début, en 1951, nous nous sommes trouvé devant un problème assez difficile, complexe et encore peu étudié. Aussi, avant de pouvoir définir une méthode de lutte biologique contre *Parlatoria blanchardi*, a-t-il fallu étudier au préalable l'écologie et la biologie de cette cochenille en Afrique du Nord en général, et au Maroc en particulier. Il a fallu déterminer ses prédateurs, la composition des espèces, connaître leur écologie et leur biologie dans les oasis d'Afrique du Nord, puis leurs relations avec *Parlatoria blanchardi*.

Nous avons observé des oasis d'Algérie et de Tunisie où l'implantation de *Parlatoria blanchardi* remonte à une époque lointaine; nous avons ainsi remarqué que, si cette cochenille est répandue, selon les endroits, en plus ou moins grand nombre sur les feuilles, elle envahit cependant rarement les fruits dans ces oasis, nous avons pu établir que les prédateurs de *Parlatoria blanchardi* dévoraient en masse les larves de la cochenille précisément à l'époque où celles-ci, peut-être à cause des phénomènes de tropisme ou d'hémitropisme, vont se porter sur les fruits mûrissants.

Au Maroc, par contre, l'invasion de *P. blanchardi* est considérable et les dommages causés aux récoltes sont graves par suite d'une part, du nombre minime de prédateurs et d'autre part de la non synchronisation de leur quantité et efficacité maxima avec les époques d'éclosion massive des œufs de la cochenille et de la fixation des larves sur les fruits. C'est pourquoi, l'on trouve si souvent des fruits recouverts d'une croûte les rendant inutilisables.

Jusqu'à présent, seules deux espèces de prédateurs de *Parlatoria blanchardi* étaient connues: *Cybocephalus palmarum* (Peyer) (Coléopt. Nitidulidae) et *Pharoscymnus anchorago* (Fairm.).

Ces prédateurs ont été signalés pour la première fois en 1924-1926 par M. A. S. Balachowsky, l'éminent entomologiste de l'Institut Pasteur de Paris qui a posé, à cette époque, le problème de l'utilisation de ces prédateurs dans la lutte contre *Parlatoria blanchardi*.

A l'heure actuelle, nous avons enregistré 35 espèces différentes de prédateurs de *P. blanchardi* avec leurs formes écologiques essentielles.

Parmi ces espèces, la première est un acarien extraordinairement actif: *Hemisarcoptes malus Shimer*. Les 34 autres espèces appartiennent aux insectes, particulièrement

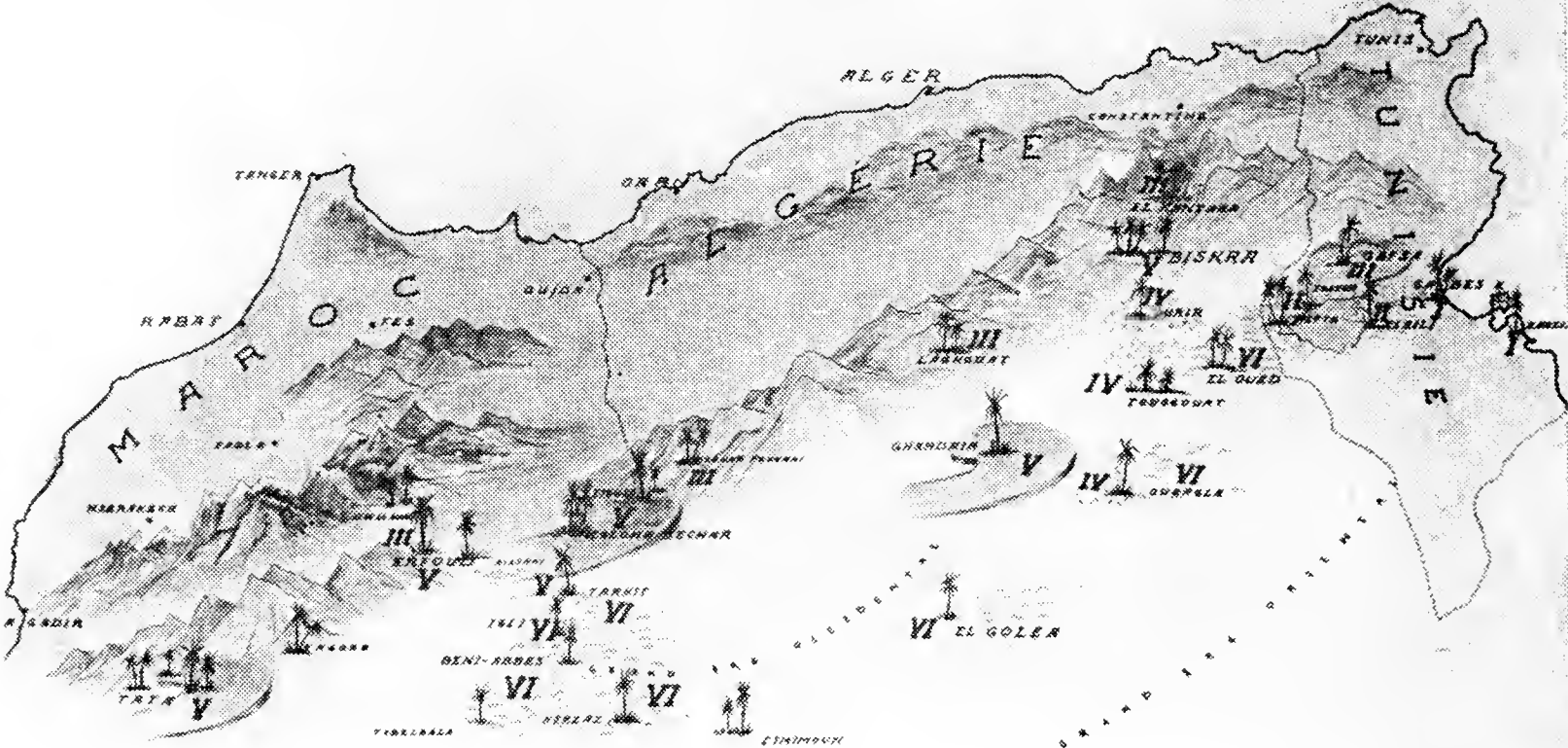
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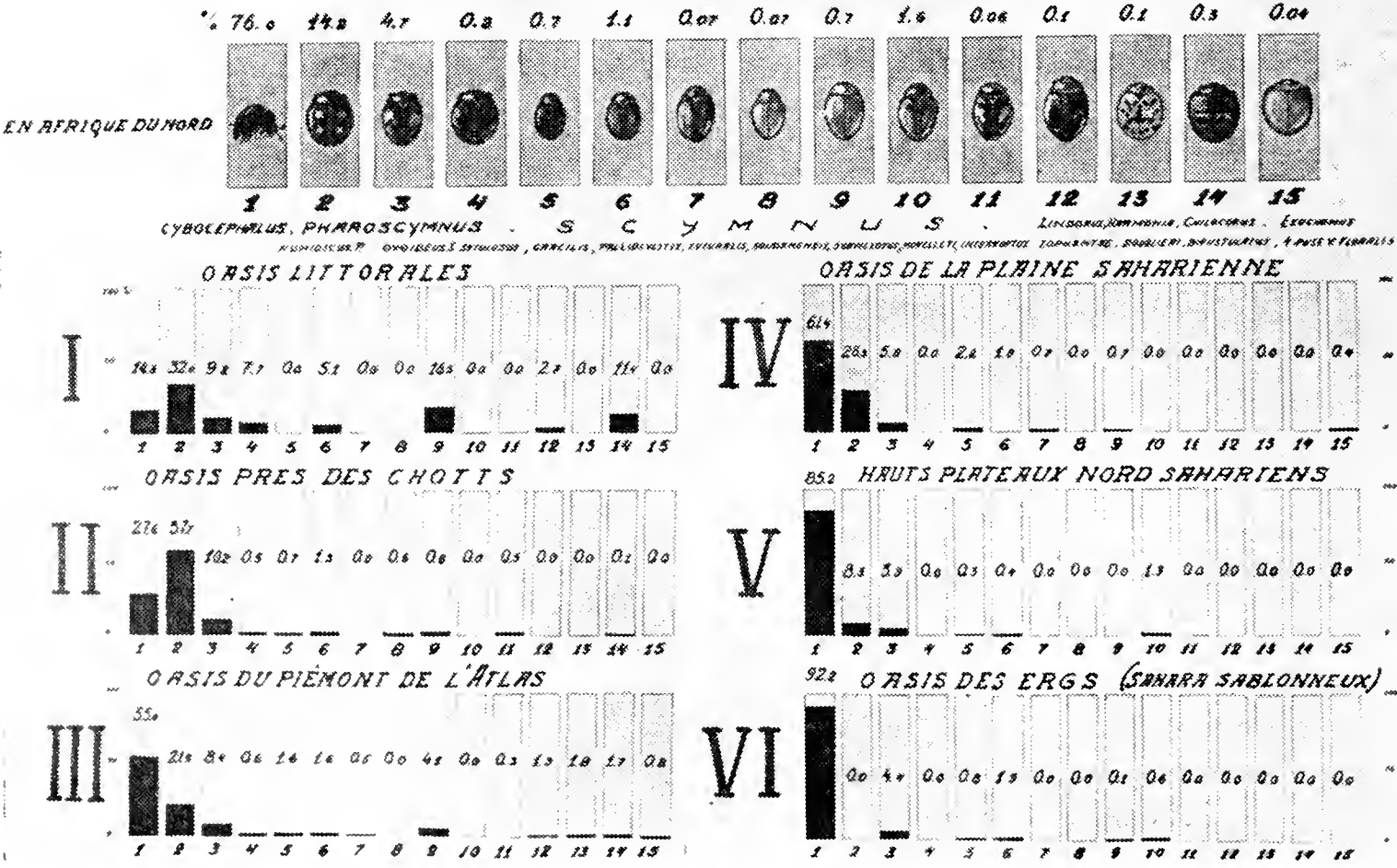
aux coléoptères; 27 d'entre elles se rangent parmi les Coccinellidae (différentes espèces de *Pharoscyms*, *Scymnus*, *Chilocorus*, *Exochomus*, etc...), 5 parmi les Nitidulidae (*Cybocephalus*). Restent 1 Planipidea de la famille des Chrysopidae et 1 Heteroptère de la famille des Anthocorides.

Pour la plupart de ces prédateurs, les caractéristiques écologistes, l'aire d'habitat et le nombre sont plus ou moins déterminés, ce qui permet déjà de juger de la plasticité écologique de telle ou telle espèce.

**DIFFERENTES OASIS DE L'AFRIQUE DU NORD**  
**CLASSEES D'APRÈS LES CONDITIONS MACRO-CLIMATIQUES**



**POURCENTAGE DE RÉPARTITION DES DIFFÉRENTES ESPÈCES**  
**DE PREDATEURS DE *PARLATORIA BLANCHARDI***



Considérons une carte de répartition géographique et des diagrammes quantitatifs concernant les principales espèces de prédateurs de *P. blanchardi* dans les oasis d'Afrique du Nord.

Nous constatons, par exemple, que *Cybocephalus* forme, dans les oasis du littoral, 14,8% de la faune des prédateurs alors que dans les oasis des Ergs (Sahara sablonneux) il constitue les 92,2% de cette faune, par contre, *Pharoscymnus numidicus*, dans les oasis près des Chotts, représente 57,7% de la faune des prédateurs de *P. blanchardi*, alors que dans les oasis des hauts plateaux nord sahariens il ne figure que pour 8,3% et qu'il est absent dans les oasis des Ergs. (Sahara sablonneux).

Ces renseignements constituent le point de départ de l'étude du problème de l'introduction de prédateurs dans les oasis du Maroc.

Dès 1952, nous avons procédé à l'acclimatation, dans les oasis, de quelques espèces de prédateurs récoltés dans l'ensemble du Maroc, y compris les régions littorales. Les espèces énumérées ci-dessous se sont acclimatées et sont entrées définitivement dans la composition de la faune de quelques oasis:

1. *Chilocorus bipustulatus* (L.).
2. *Lindorus lophantae* (Blaisd.) (Tafilalet).
3. *Scymus pallidivestis* (Muls.).
4. *Scymus subvillosus* forme *pubescens* (Panzer).

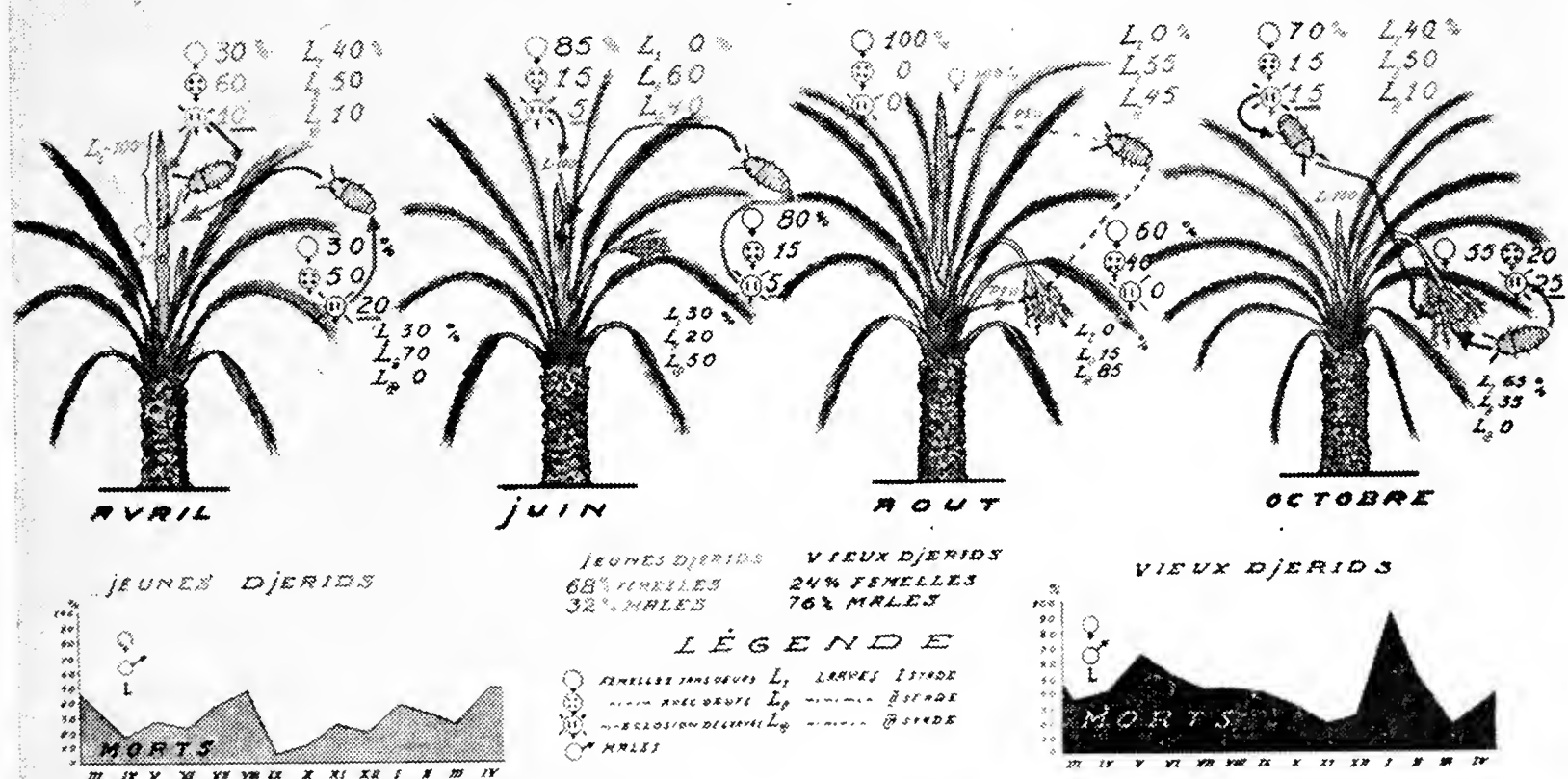
Par contre, ne se sont pas acclimatés:

1. *Scymus luteus* (Sic.).
2. *Coccinella 22 punctata* (L.).
3. *Rhizobius litura* (F.).

En décembre 1954, nous avons reçu une colonie comprenant 625 imago de *Chilocorus cacti* en provenance du Texas (Nous exprimons à ce sujet nos remerciements à M.M. les Professeurs C. P. Clausen et T. R. Gardner, Citrus Experiment Station — California). Cette espèce de Coccinellidae, qui auparavant n'existait pas au Maroc, s'est très bien acclimatée et multipliée dans une petite oasis isolée du Tafilalet: elle est prête actuellement à être transférée dans d'autres oasis.

En Avril 1954, dans des endroits préalablement contrôlés et spécialement repérés de certaines oasis algériennes, nous avons procédé, sur une grande échelle à une récolte

## SCHEMA DES MIGRATIONS SAISONNIERES DES LARVES DE *P. BLANCHARDI* SUR UN PALMIER



W. SMIRNOFF.

de prédateurs. Quelques millions d'individus, appartenant à 14 espèces diverses ont pu être expédiés par avion et lâchés dans des endroits spécialement choisis dans plusieurs oasis du Maroc.

Les prédateurs étaient arrivés en bon état. Quelques mois plus tard, on pouvait apercevoir déjà des résultats satisfaisants et juger de la bonne adaptation des prédateurs à leur nouvel habitat.

L'étape suivante consistait à répartir les prédateurs ainsi acclimatés dans les diverses oasis où ils n'étaient pas encore parvenus par leurs propres moyens. Nous avons introduit ces prédateurs dans les oasis où l'invasion de *Parlatoria blanchardi* n'est qu'à ses débuts; nous avons poussé l'expérience jusqu'aux oasis non encore atteintes par *Parlatoria blanchardi* mais où existent sur des plantes autres que le palmier d'autres espèces de cochenilles qui puissent servir de nourriture à ces prédateurs et maintenir leur présence dans la faune des oasis avant l'invasion de la cochenille. (A ce stade, notre travail n'est encore qu'expérimental).

La récolte et le transfert des prédateurs à l'intérieur des oasis ou d'une oasis à l'autre est effectuée avec intérêt par les élèves des écoles locales sous la conduite de leurs maîtres.

Deux années se sont écoulées depuis l'introduction de ces prédateurs; on peut déjà observer, par endroits, une nette régression de la cochenille sur les palmiers. En bien des endroits, la cochenille n'atteint plus les fruits qui ont à nouveau retrouvé, de ce fait, leur valeur marchande et alimentaire.

# The Control of *Aphis fabae* Scop. with Special Reference to Biological Control of Insects Which Attack Annual Crops

By M. J. WAY and C. J. BANKS

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## ABSTRACT

*Aphidae* by their powers of rapid reproduction and efficient dispersal seem well adapted to annual hosts. Chemicals are widely used to control them but relatively little is known about their control by natural enemies or about the effect of chemicals on this. This paper describes techniques being used in an attempt to evaluate the effects of natural enemies on populations of *Aphis fabae* Scop. Where relevant, chemical and biological controls are compared. First results indicate that, when the aphid is on an annual crop in midsummer, its predators and parasites are a minor factor in its control and chemical control is necessary if an attack develops. From August to the following May *A. fabae* is on weeds and shrubs often in natural or semi-natural environments. Here, predators and parasites may be a major controlling factor and hence may determine the number of migrant aphids which in May and June depart to the midsummer host. This is important because the size of the aphid population which develops on the midsummer host and the crop loss are directly related to the number of migrants reaching it.

Insecticides applied to the midsummer host plant deplete the predator population available to attack the aphid on its later hosts. This could have harmful effects.

There are many reports of pest outbreaks following the use of chemical sprays and dusts (Solomon, 1953; Ripper, 1956) and it has been shown with some perennial tree crop pests that these outbreaks may be caused by the chemical killing the pests' natural enemies (Pickett & Patterson, 1953; DeBach & Bartlett, 1951; Massee, 1953; Collyer, 1953). It should not be assumed, however, that natural enemies are equally effective in suppressing pests or potential pests of crops other than some perennials. This is supported by the results of biological control using introduced natural enemies which have been most successful against pests of certain perennial tree crops (Koebele, 1890; Tothill and others, 1930; Taylor, 1937).

A tree crop forms a relatively stable habitat for phytophagous insects and their enemies, many of which overwinter on the trees or undergrowth, emerge together at about the same time in spring and are able to attain an equilibrium which, if disturbed by chemicals, can lead to pest outbreaks.

Conditions in annual field or truck crops are strikingly different. There is no stable environment for the insect fauna because periods when the soil is bare of vegetation alternate with periods when it is planted with a crop, perhaps entirely different from the previous one; also, the crop may be suitable for only part of its short growing season. There can be no resident insect population except in the soil and a fresh community develops annually on each crop, much of it by migration from outside.

Although the difference between these two kinds of man-made environment is not a rigid one, the instability of the annual crop habitat is such that entomophagous insects are likely to be less effective than in the more stable perennial crop, and it is therefore less likely that chemicals will have harmful effects.

There is little quantitative information on how entomophagous insects affect pests of annual crops and an attempt is being made at Rothamsted to investigate this problem beginning with the black bean aphid, *Aphis fabae* Scop. and its complex of natural enemies.

*A. fabae* with its efficient means of dispersal and powers of rapid reproduction seems well adapted to exploit the annual crop habitat. In Great Britain it may be a serious pest of beans and sugar beet during the months June to August. It lives on various weeds from August to October and passes the winter in the egg stage on the shrub *Euonymus europaeus*.



Natural populations of the aphid and of its parasites and predators are being recorded on the various host plants throughout the year. Experimental populations are also being studied using caged plots of the host plants artificially infested with equal number of aphids. Parasites and predators are excluded from some cages by dieldrin-treated terylene netting, a method essentially similar to that of DeBach, Dietrick and Fleschner (1949). Other cages giving comparable climatic conditions have slatted walls which allow the free access of naturally-occurring parasites and predators.

Results obtained so far suggest that abundant predators which reach maturity on big aphid populations developing on the mid-summer host plant have relatively little effect on the aphids at the time; but on other host plants later in the year and during the following spring they and their progeny may suppress the aphid population sufficiently to prevent an outbreak in the second year. A cycle of large and small populations in alternate years would, therefore, be expected if numbers of *A. fabae* were regulated solely by natural enemies. This does not always occur because other regulating factors are sometimes important. Natural enemies are, however, potentially important in a year following one when big aphid populations developed.

There is a possibility that chemical control measures, used extensively during years of heavy aphid attack, would seriously reduce the numbers of the beneficial entomophagous insects, for, even if they were not killed by the spraying, they would be deprived of prey on which to multiply. A consequence might be that every year could become one of heavy aphid attack. Further information is needed on these problems, not only for *A. fabae* but also for the complex of aphid species which occur in the same habitats and which are attacked by the same predators.

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## DISCUSSION

W. E. RIPPER. While congratulating Dr. Way on the results of experimental data, his general remark about the lack of resurgences is contradicted by many references in literature to resurgences of cotton pests and even *Aphis fabae* after parathion spraying and contact insecticides.

M. J. WAY. My experience is limited and I agree that in years of light aphid attack, specific destruction of natural enemies by an insecticide can increase the aphid population; but such a resurgence will only occur if the aphid population is controlled inefficiently. An efficient aphicide like demeton kills many insect enemies but in my experience, it gives better control on an annual crop than less efficient aphicides, which leave the predators unharmed.

G. J. KERRICH. To what extent are the three main predators of *Aphis fabae*, the coccinellid, syrphid, and anthocorid, polyphagous and can they not build up their populations on other aphids or other plants in alternate years?



M. J. WAY. They appeared to be associated with the field and hedgerow habitat and fed on other aphids in this habitat. The populations of some of these aphids fluctuate like that of *Aphis fabae* and hence would fit into the suggested picture. It is vital that we should study the whole complex of aphids which live in this habitat.



# An Attempt in South Africa to Control the Koroo Caterpillar Biologically

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Pretoria, South Africa

The title of this paper has been changed because that given in the official programme of the Congress is misleading. It will not be possible to give details of the whole project here but these are being published in a comprehensive bulletin by Bedford and the present author.

All I can hope to do now is to show you briefly why Biological Control was attempted in this case and why it apparently has failed.

The Koroo is a large arid, semidesert region in South Africa in which our sheep and wool industry has flourished. It is a summer rainfall area from 3 to 5 thousand feet above sea level and is subject to severe droughts which may last for three or four years. The natural vegetation — and the indigenous animals — are specially adapted to survive these droughts and the grazing for sheep consists mainly of Koroo bushes. The most important of these is *Pantzia incana*, called by the farmers the Sweet Koroo. This is a low-growing bush with succulent leaves. During droughts it loses its leaves and appears to be quite dead, its branches being dry and brittle. As soon as the torrential rains come in the summer, however, it makes a miraculous recovery and in about two weeks the veld appears a rich dark green with plenty of excellent feed for the sheep. This veld will then often support the flocks for many months without further rains.

Very often, however, and just as the veld is at its best, the Koroo caterpillar (*Loxostege frustalis*) appears in great numbers, covers the bushes with a fine web and defoliates them so that, as the farmers say, the condition of the veld is soon worse than it was before the rains.

Because of the size of the farms and the vast area of the Koroo, chemical control seemed out of the question and it was decided to attempt the control of this indigenous insect biologically.

I would like here to pay a tribute to the late Dr. Ulliyett who started this project and inspired us all in the Division of Entomology with his wonderful enthusiasm. It was suggested that *Chelonus texanus*, a parasite of the beet webworm, *L. sticticalis* be introduced from America. As the two pests belong to the same genus there seemed every reason to think that the project would be successful. Moreover, preliminary tests in cages showed that *C. texanus* would attack *L. frustalis* and would develop in it. Ulliyett also found that the parasite would breed freely in the Mediterranean meal moth, *Ephestia kühniella*.

He developed the laboratory technique for mass-breeding *Chelonus* in *Ephestia* as a laboratory host which is shown in the film and we equipped two old buildings and had a staff of about 15 people at one time on this work. Koroo bushes grow slowly and are difficult to grow under artificial conditions as also are the Koroo caterpillars so that it would be a very laborious task to rear large numbers of *Chelonus* on them in the laboratory. The meal moth on the other hand is comparatively easy to rear. *Chelonus* attacks the eggs of its host by ovipositing in them. The host eggs hatch normally and the resulting caterpillars feed until they are full grown and ready to pupate. They even spin their cocoons, but by this time the developing parasite larva inside them has become full grown, devoured its host and pupates itself inside the host cocoon.

The rearing work was carried on at our Sunnyside Parasite Laboratory for four years by Ulliyett and five years after he left us — nearly ten years altogether — during which time nearly eight million *Chelonus* parasites were produced and distributed in the Koroo area. They were shipped in special ice cooled boxes to selected farmers who sent in weather reports and released the wasps just when, according to our estimates, there was a maximum number of *Loxostege* eggs available.

At first we were very optimistic, especially when a few *C. texanus* wasps were recovered from caterpillars collected in the veld. This was however during the same summer and, only a few weeks after the parasites had been released.

Later more *Chelonus* were recovered but it was found to our consternation that these belonged to another species. They were identified as *C. curvimaculatus* which turned out to be an indigenous species having very little effect on the populations of *Loxostege*. Further study showed that our *Loxostege* goes into a long diapause of up to five years during droughts and that the imported parasite was not able to follow its new host through such periods. No further *C. texanus* wasps have been recovered and apparently the whole project has been a failure from the practical point of view.

There are at least three lessons which we can learn from this project:—

1. We should have done much more preliminary survey work before introducing *Chelonus*. *C. curvimaculatus* is usually very scarce and difficult to find but it might then have been discovered and much confusion avoided.

2. More information about the Koroo caterpillar should have been gathered. In those days, however, we knew very little about diapause.

3. We cannot tell from laboratory observations and experiments in cages what the habits of a parasite will be in the field. It is only by patient field observations that we can see what such a parasite as *Chelonus* will actually do and how efficient it is in finding the eggs of its host.

There are, of course, other factors such as the attack of ants but there is not time to discuss these here.

#### DISCUSSION

G. J. KERRICH. Commented that diapause in the holarctic region was usual over one winter, frequent over two winters, and, according to F. J. Simmonds, known over three; but diapause over four or five winters must surely be a special adaptation. Was anything known about this in the other parasites, primary and hyper? Were these other parasites frequent or were they hard to collect?

B. SMIT. This I cannot answer. The host larva rests in its cocoon in the soil, four or five years. I do not know enough about the hypers to say. The indigenous parasites are hard to collect, but we now have about 40,000 *Loxostege* cocoons that have been under observation for nearly five years. Moths and parasites are still emerging.

K. S. HAGEN. In what stage does the *C. texanus* die in the host larvae?

B. SMIT. This I cannot answer. The host larva rests in its cocoon in the soil, sometimes for three or four years and we have not collected and dissected enough of them at different stages to be able to answer this question.

F. J. SIMMONDS. *C. texanus* occurs in Alberta where conditions are very much more severe than in the Karoo; it synchronizes well with its host, *Loxostege sticticalis*. Also, *Chelonus* is not the most important parasite of this host in Alberta.

B. SMIT. We did introduce *Bracon vulgaris* but did not breed it. It also has apparently died out. The diapause in the case of *L. frustalis* is very long, often four or five years. Perhaps this has something to do with it. It is also, of course, possible that we may still find that *C. texanus* has survived.

# Primer Catalogo de los Parasitos y Predadores Encontrados en el Uruguay

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y

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Este catálogo tiene como objeto el ordenar taxonómicamente los insectos parásitos y predadores de insectos indígenas o establecidos, encontrados hasta el presente en la República Oriental del Uruguay.

Varias de las especies mencionadas han sido constatadas en investigaciones realizadas por el *South American Parasite Laboratory (Bureau of Entomology and P. Quarantine, U. S. D. A.)* para el cual trabajó uno de los autores (A. S. G.). Las especies restantes se obtuvieron del producto de investigaciones realizadas por la Cátedra de Entomología de la Facultad de Agronomía, por la División Zoología Agrícola de la Dirección de Agronomía (Ministerio de Ganadería y Agricultura), y por la Oficina Nacional del Servicio de Lucha Contra la Langosta (Ministerio de Ganadería y Agricultura).

Buena parte del material citado en este trabajo se encuentra en el United States National Museum, Cátedra de Entomología de la Facultad de Agronomía, División Zoología Agrícola de la Dirección de Agronomía, colecciones particulares de los Dres. Everardo E. Blanchard, Luis De Santis y Juan M. Bosq.

En la cría de los insectos parásitos y predadores que se mencionan, han intervenido, además de los autores, los siguientes investigadores: Dr. Harry L. Parker, D. Paul Berry, Ings. Agrs. Carlos S. Carbonell, F. Mesa Carrión, Agustín Trujillo Peluffo, Dr. D. C. Lloyd, Bachs. Alejo Mesa, Joaquín Carbonell y Omar Núñez.

Deseamos expresar nuestro reconocimiento, por contribuir en la identificación del material entomológico, hacia el Dr. H. L. Parker, especialistas del National Museum U. S. D. A., Everardo E. Blanchard, Luis De Santis, Angelo M. da Costa Lima, Juan M. Bosq, Dr. Alejandro Ogloblin y Paul Berry.

## HOSPEDANTES - PARASITOS Y PREDADORES

### ARACHNIDA

Araneida pl. sp.

*Pepsis* pl. sp. (Hym., Pompilidae).  
Montevideo.

Araneida sp.

Pompilidae sp. (Hym.). Montevideo.

*Bryobia praetiosa* Koch. (Acarina,  
Tetranychidae).

*Eriopsis connexa* (Germ.) (Col.,  
Coccinellidae). Montevideo.

### COLEOPTERA

*Acanthoscelides spinipes* (Erich.)  
(Bruchidae).

*Horismenus* sp. (Hym., Eulophidae).  
Colonia, San José.

*Lariophagus* sp. (Hym., Pteromalidae).  
Colonia, San José.

*Achryson undulatum* Burm. (Cerambycidae).

*Doryctes* sp. (Hym., Braconidae).  
Montevideo.

*Ipobracon* sp. (Hym., Braconidae).  
Montevideo.

*Anacassis prolixa* (Boh.) (Chrysomelidae).

*Eucelatoriopsis* sp. nov. (Dip.,  
Tachinidae). Montevideo.

*Tachynophytopsis* sp. (Dip., Tachinidae).  
Montevideo.

*Apion* sp. (Curculionidae).

*Eupelmus cushmani* Cwfd. (Hym.,  
Eupelmidae). Canelones (Pando).  
Montevideo (Carrasco).

*Eurytoma* sp. (Hym., Eurytomidae).  
Montevideo (Carrasco).

Bruchidae sp.

*Metastenus* sp. (Hym., Pteromalidae).  
Colonia (Carmelo).

*Bruchus rufimanus* Boh. (Bruchidae).

*Triaspis thoracicus* (Curt.) (Hym.,  
Braconidae). San José (Libertad).

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## COLEOPTERA (cont.)

- Calandra granaria* L. (Curculionidae)  
*Chaetospila elegans* Westw. (Hym.,  
Pteromalidae). Montevideo.  
*Lariophagus distinguendus* (Försk.) (Hym.,  
Pteromalidae). Montevideo.
- Calandra oryzae* L. (Curculionidae)  
*Chaetospila elegans* Westw. (Hym.,  
Pteromalidae). Montevideo.  
*Lariophagus distinguendus* (Försk.) Hym.,  
Pteromalidae). Montevideo.
- Cassididae sp.  
*Spilochalcis chapadae* Ashm. (Hym.,  
Chalcididae). Montevideo.
- Chelymiorpha variabilis* Boh. (Cassididae)  
*Emersonella niveipes* Gir. (Hym.,  
Eulophidae). Río Negro (Young).  
*Eucelatoriopsis* sp. nov. (Dip., Tachinidae).  
Montevideo.
- Chrysomelidae sp.  
*Doryphorophaga* sp. (Dip., Tachinidae).  
Montevideo.
- Ciidae gen. ign.  
*Cephalonomia* sp. (Hym., Bethyridae).  
Montevideo.  
Eulophidae gen. ign. (Hym.)  
Montevideo.  
*Eupelmus cushmani* Cwfd. (Hym.,  
Eupelmidae). Montevideo.
- Coccinellidae sp.  
*Homalotylus mirabilis* Brèthes (Hym.,  
Encyrtidae). San José.  
*Homalotylus terminalis* Say (Hym.,  
Encyrtidae). Salto.
- Conotrachelus cristatus* Fahr. (Curculionidae)  
*Microbracon* sp. (Hym., Braconidae).  
Colonia (Colonia Suiza).  
*Pseudoclista* sp. aff. *atra* B. & B. (Dip.,  
Tachinidae). Colonia (Colonia Suiza).  
*Triaspis* sp. nov. 1 (Hym., Braconidae).  
Montevideo.  
*Triaspis* sp. nov. 2 (Hym., Braconidae).  
Montevideo.
- Conotrachelus subnebulosus* Hust.  
(Curculionidae)  
*Euzenilliopsis* gen. aff. (Dip., Tachinidae).  
Colonia, Florida.  
*Euzenilliopsis* sp. (Dip., Tachinidae).  
Florida.  
*Pseudoclista* sp. aff. *atra* B. & B. (Dip.,  
Tachinidae). Colonia (Colonia Suiza).  
*Triaspis* sp. nov. (Hym., Braconidae).  
Colonia (Colonia Suiza), Montevideo.
- Conotrachelus* sp. (Curculionidae)  
*Microbracon* sp. (Hym., Braconidae).  
Colonia (Colonia Suiza).
- Cybocephalus* sp. (Cybocephalidae)  
*Zatropis* sp. (Hym., Pteromalidae). Colonia  
(Colonia Suiza).
- Cyclocephala signaticollis* Burm. (Dynastidae)  
*Rhamphina* sp. aff. *argentina* Bigot (Dip.,  
Tachinidae). Canelones, Soriano.
- Cyclocephala* sp. (Dynastidae)  
Cantharidae gen. ign. (Col.).  
Canelones.  
*Leptocera* sp. (Dip., Leptoceridae).  
Canelones.
- Prorhyncops* sp. nov. (Dip., Tachinidae).  
Canelones.  
*Ptilodexia* sp. (Dip., Tachinidae).  
Canelones.
- Cycloneda sanguinea* (L.) (Coccinellidae)  
*Homalotylus flaminus* (Dalm.) (Hym.,  
Encyrtidae). Montevideo (Sayago).  
*Perilitus coccinellae* Schrank (Hym.,  
Braconidae). Montevideo.
- Diabrotica speciosa* (Germ.) (Galerucidae)  
*Celatoria bosqui* Blnchd. (Dip.,  
Tachinidae). Colonia, Montevideo.
- Diloboderus abderus* (Sturm.) (Dynastidae)  
*Leptocera* sp. (Dip., Leptoceridae).  
Canelones.
- Prorhyncops* sp. (Dip., Tachinidae).  
Canelones.
- Rhamphina* sp. aff. *argentina* Bigot (Dip.,  
Tachinidae). Maldonado.
- Tiphia* sp. (Hym., Tiphidae). Paysandú.
- Gonipterus gibberus* (Boisd.)  
(Curculionidae)  
*Podisus australis* Berg (Hem.,  
Pentatomidae). Montevideo.
- Yungaburra nitens* (Gir.) (Hym.,  
Mymaridae). Montevideo.
- Lasioderma serricorne* Fabr. (Anobiidae)  
*Lariophagus distinguendus* (Försk.)  
(Hym., Pteromalidae). Montevideo.
- Lema bilineata* (Germ.) (Crioceridae)  
*Emersonella* sp. (Hym., Eulophidae).  
Montevideo.
- Hemiargyropsis* sp. (Dip., Tachinidae).  
Montevideo.
- Paradoria* sp. (Dip., Tachinidae).  
Montevideo.
- Listroderes costirostris obliquus* (Klug)  
(Curculionidae)  
*Epiplagiops littoralis* Blnchd. (Dip.,  
Tachinidae). Canelones, Montevideo.
- Porizon argentinensis* Blnchd. (Hym.,  
Ichneumonidae). Canelones,  
Montevideo.
- Porizon parkeri* Blnchd. (Hym.,  
Ichneumonidae). Canelones,  
Montevideo, San José (Libertad).
- Triaspis* sp. nov. (Hym., Braconidae)  
Montevideo, Rocha.
- Listroderes* pl. sp. (Curculionidae)  
*Epiplagiops littoralis* Blnchd. (Dip.,  
Tachinidae). Canelones, Montevideo.
- Listroderes* sp. (Curculionidae)  
Mermittidae sp. (Nematoda).  
Montevideo.
- Triaspis* sp. nov. (Hym., Braconidae).  
Montevideo, Rocha.
- Megacyllene* sp. (Cerambycidae)  
*Doryctes* sp. (Hym., Braconidae).  
Montevideo.
- Ipobracon* sp. (Hym., Braconidae).  
Montevideo.
- Metallactus pollens* Sffr. (Clytridae)  
Pteromalidae gen. ign. (Hym.)  
Montevideo.
- Microtheca ochroloma* Stal (Chrysomelidae)  
*Doryphorophaga* sp. (Dip., Tachinidae).  
Montevideo.

## COLEOPTERA (cont.)

- Microtheca semilaevis* Stal (Chrysomelidae)  
*Doryphorophaga* sp. (Dip., Tachinidae).  
 Montevideo.  
*Polyspila polyspila* (Germ.) (Chrysomelidae)  
*Austrolydella* sp. aff. *assimilis* Tns. (Dip.,  
 Tachinidae). Montevideo.  
*Epiplagiops littoralis* Blnchd. (Dip.,  
 Tachinidae). Montevideo.  
*Metadoria* sp. (Dip., Tachinidae).  
 Montevideo.

- Scarabaeidae sp.  
*Erax* pl. sp. (Dip., Asilidae). Montevideo.  
*Holcocephala uruguayensis* E. Lynch A.  
 (Dip., Asilidae). Montevideo.  
*Mallophora ruficauda* Wied. (Dip.,  
 Asilidae). Colonia.  
*Uroxys* sp. (Scarabaeidae)  
*Eupelmus cushmani* Cwfd. (Hym.,  
 Eupelmidae). Canelones (Pando).

## DIPTERA

- Agromyzidae sp.  
*Achrysocharella* sp. nov. (Hym.,  
 Eulophidae). Montevideo.  
*Allograpta exotica* (Wied.) (Syrphidae)  
*Diplazon laetatorius* (Fabr.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Allograpta* sp. aff. *obliqua* Say (Syrphidae)  
*Diplazon laetatorius* (Fabr.) (Hym.,  
 Ichneumonidae). Río Negro (Young).  
*Allograpta* sp. (Syrphidae)  
*Pachyneuron* sp. (Hym., Pteromalidae).  
 Montevideo.  
*Anastrepha fraterculus* (Wied.) (Trypetidae)  
*Eucoila haywardi* Blnchd. (Hym.,  
 Eucoilidae). Salto.  
Cecidomyiidae gen. ign.  
*Tetrastichus* sp. (Hym., Eulophidae).  
 Canelones.  
*Zatropis* sp. (Hym., Pteromalidae).  
 Canelones.  
Diptera sp.  
*Brachymeria* sp. (Hym., Chalcididae).  
 Montevideo.  
*Drosophila* sp. (Drosophilidae)  
*Opius* sp. nov. (Hym., Braconidae).  
 "Parasite of this diptera in bulk material  
 of *Lecanium perinflatum* Ckll." (Parker,  
 Berry & Silveira). Colonia (Carmelo),  
 Montevideo.  
*Eucelatoriopsis* sp. (Tachinidae)  
*Brachymeria* sp. (Hym., Chalcididae).  
 Montevideo.

- Brachymeria subrugosa* Blnchd. (Hym.,  
 Chalcididae). Montevideo.  
*Hydrellia griseola* (Fall.) (Ephydriidae)  
*Achrysocharis* sp. (Hym., Eulophidae).  
 Treinta y Tres (Laguna Merim).  
*Opius* sp. (Hym., Braconidae). Treinta y  
 Tres (Laguna Merim).  
*Pteromalus* sp. (Hym., Pteromalidae).  
 Treinta y Tres (Laguna Merim).  
*Liriomyza pusilla* (Meig.) (Agromyzidae)  
*Derostenus* sp. (Hym., Eulophidae).  
 Montevideo (Sayago).  
*Opius* sp. nov. (Hym., Braconidae).  
 Montevideo (Sayago).  
*Solenotus* sp. (Hym., Eulophidae).  
 Montevideo (Sayago).

- Syrphidae sp.  
*Diplazon laetatorius* (Fabr.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Ethelurgus* sp. aff. *syrphicola* (Ashm.)  
 (Hym., Ichneumonidae). San José.  
*Pachyneuron* sp. (Hym., Pteromalidae).  
 Montevideo.  
*Voria ayerzai* Brèthes (Tachinidae)  
*Brachymeria ovata* Say (Hym.,  
 Chalcididae). Durazno (Blanquillo).  
*Eupelmus elegans* Blnchd. (Hym.,  
 Eupelmidae). Durazno (Blanquillo).  
*Voria brasiliiana* Tns.  
*Brachymeria ovata* Say (Hym.,  
 Chalcididae). Florida.

## HEMIPTERA

- Acanonicus hahni* (Stal) (Coreidae)  
*Hadronotus* sp. (Hym., Scelionidae).  
 Montevideo.  
*Trichopoda* sp. (Dip., Tachinidae).  
 Montevideo.  
*Acladra* sp. (Pentatomidae)  
*Telenomus* sp. (Hym., Scelionidae).  
 Paysandú.  
Coreidae gen. ign.  
*Telenomus* sp. (Hym., Scelionidae).  
 Montevideo.  
*Edessa mediatubunda* (Fabr.) (Pentatomidae)  
*Neobrachelia* sp. (Dip., Tachinidae).  
 Montevideo.  
*Trissolcus* sp. (Hym., Scelionidae).  
 Montevideo.  
*Xenopyxis edessae* Tns. (Dip.,  
 Tachinidae). Montevideo.  
*Edessa rufomarginata* (De Geer)  
 (Pentatomidae)  
*Neobrachelia* sp. (Dip., Tachinidae).  
 Montevideo.  
*Telenomus* sp. (Hym., Scelionidae).  
 Colonia.

- Xenopyxis edessae* Tns. (Dip.,  
 Tachinidae). Montevideo.  
*Nezara viridula* (L.) (Pentatomidae)  
*Eutrichopoda* sp. (Dip., Tachinidae). Río  
 Negro.  
*Mallophora ruficauda* Wied. (Dip.,  
 Asilidae). Canelones, Montevideo.  
*Milichiella* sp. (Dip., Milichiidae).  
 Montevideo.  
Pentatomidae sp.  
*Hadronotus* sp. (Hym., Scelionidae).  
 Colonia, Soriano (Mercedes).  
*Trissolcus* sp. (Hym., Scelionidae).  
 Colonia, Montevideo (Carrasco).  
*Trissolcus urichii* Cwfd. (Hym.,  
 Scelionidae). Colonia.  
*Solubea poecila* (Dall.) (Pentatomidae)  
*Telenomus mormideae* Costa Lima (Hym.,  
 Scelionidae). Artigas.  
*Solubea ypsilon-griseus* De Geer  
 (Pentatomidae)  
*Telenomus mormideae* Costa Lima (Hym.,  
 Scelionidae). Artigas.

## HOMOPTERA

- Akermes bruneri* Ckll. (Coccidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Canelones, Colonia, Paysandú, Soriano.  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Canelones (Pando).  
*Coccophagus saissetiae* Gah. (Hym., Aphelinidae). Paysandú.  
*Laetitia* sp. (Lep., Phycitidae). (Predator-Inquilino). Soriano (Mercedes).  
*Aleurothrixus floccosus* (Mask.) (Aleyrodidae)  
*Amitus* sp. (Platygasteridae). Montevideo.  
*Cales noacki* How. (Hym., Aphelinidae). Montevideo.  
*Aleurothrixus* sp. (Aleyrodidae)  
*Amitus* sp. (Hym., Platygasteridae). Montevideo.  
*Alichtensia orientalis* Lah. (Coccidae)  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Coccophagus scutellaris* Dalm. (Hym., Aphelinidae). Montevideo.  
*Coccophagus* sp. (Hym., Aphelinidae). Montevideo.  
*Laetilia* sp. (Lep., Phycitidae). "Larva is inquiline-predator on scale" (Parker, Berry & Silveira). Soriano (Mercedes).  
Aphididae pl. sp.  
*Allograpta exotica* (Wied.) (Dip., Syrphidae). Montevideo.  
*Ceratomegilla quadrifasciata* Schönh. a. *octodecimpustulata* Muls. (Col., Coccinellidae). Montevideo.  
*Chrysopa lanata* Banks (Neur., Chrysopidae). Montevideo.  
*Coccinella ancoralis* (Germ.) (Col., Coccinellidae). Montevideo.  
*Cycloneda sanguinea* (L.) (Col., Coccinellidae). Montevideo.  
*Eriopis connexa* (Germ.) (Col., Coccinellidae). Montevideo.  
*Scymnus argentinus* Ws. (Col., Coccinellidae). Montevideo.  
*Tubifera furcata* (Wied.) (Dip., Syrphidae). Montevideo.  
Aphididae sp.  
*Mesogramma* sp. (Dip., Syrphidae). Río Negro.  
*Aphis gossypii* Glov. (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Montevideo.  
*Aphis laburni* Kalt. (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Colonia (Estanzuela).  
*Aphis pseudopomi* Blnchd. (Aphididae)  
*Scymnus argentinus* Ws. (Col., Coccinellidae). Montevideo.  
*Aspidiotus* sp. (Diaspididae)  
*Thysanus* sp. (Hym., Encyrtidae). Montevideo.  
*Aulacorthum convulvi* Kalt. (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Montevideo.  
*Brevicoryne brassicae* (L.) (Aphididae)  
*Allograpta* sp. aff. *obliqua* (Say) (Dip., Syrphidae). Montevideo.  
*Charips brassicae* Ashm. (Hym., Charipidae). "Ex material, probably hyperparasite via *Diaeretus plesiorapae* Blnchd." (Parker, Berry & Silveira). Colonia, Montevideo.  
*Diaeretus plesiorapae* Blnchd. (Hym., Aphidiidae). Colonia, Montevideo.  
*Diaeretus rapae* (Curt.) (Hym., Aphidiidae). Colonia, Montevideo.  
*Cerococcus baccharidis* (Hemp.) (Asterolecaniidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Montevideo.  
*Coccidoxenus* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Coccidencyrtus* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Coccophagus fallax* Comp. (Hym., Aphelinidae). Montevideo (Carrasco).  
*Eupelmus coccidivorus* Gah. (Hym., Eupelmidae). Montevideo.  
*Cerococcus* sp. (Asterolecaniidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Montevideo.  
*Coccidencyrtus* sp. (Hym., Encyrtidae). Montevideo.  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo (Carrasco), Maldonado.  
*Coccophagus* sp. (Hym., Aphelinidae). Montevideo.  
*Gahaniella saissetiae* Timb. (Hym., Encyrtidae). Montevideo.  
*Ceroplastes* pl. sp. (Coccidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Colonia, Montevideo, Paysandú, Soriano.  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo (Carrasco).  
*Coccophagus fallax* Comp. (Hym., Aphelinidae). Montevideo (Carrasco).  
*Coccophagus scutellaris* Dalm. (Hym., Aphelinidae). Montevideo.  
*Gahaniella saissetiae* Timb. (Hym., Encyrtidae). Canelones (Pando).  
*Pycnocephalus argentinus* Brèthes (Col., Nitidulidae). Maldonado.  
*Tetrastichus chapadae* Ashm. (Hym., Eulophidae). Montevideo.  
*Ceroplastes rusci* (L.) (Coccidae)  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Tetrastichus minutus* How. (Hym., Eulophidae). Montevideo.  
*Tetrastichus zemani* Brèthes (Hym., Eulophidae). Montevideo.  
*Ceroplastes* sp. aff. *floridensis* Comst. (Coccidae)  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Ceroplastes* sp. (Coccidae)  
*Acerophagus* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Adelencyrtus* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Aphycus* sp. (Hym., Encyrtidae). Canelones (Pando).

## HOMOPTERA (cont.)

- Aphytis* sp. nov. (Hym., Aphelinidae).  
 Montevideo.  
*Coccidencyrtus* sp. (Hym., Encyrtidae).  
 Montevideo.  
*Coccidoxenus* sp. (Hym., Encyrtidae).  
 Montevideo.  
*Coccophagus saissetiae* Gahan (Hym.,  
 Aphelinidae). Colonia (Rosario),  
 Soriano (Mercedes).  
*Coccophagus* sp. (Hym., Aphelinidae).  
 Montevideo (Carrasco).  
*Echtroplexiella* sp. (Hym., Encyrtidae).  
 Montevideo.  
*Eupelmus coccidivorus* Gah. (Hym.,  
 Eupelmidae). Montevideo.  
*Laetilia* sp. (Lep., Phycitidae). (Predator-  
 Inquilino). Soriano (Mercedes).  
*Lecaniobius* sp. nov. (Hym., Eupelmidae).  
 Colonia.  
*Leucopis griseola* Fall. (Dip.,  
 Chamaemyiidae). Montevideo.  
*Leucopis nigricornis* Egger. (Dip.,  
 Chamaemyiidae). Montevideo.  
*Leucopis* sp. nov. (Dip.,  
 Chamaemyiidae). San José.  
*Pauridia* sp. (Hym., Encyrtidae).  
 Montevideo (Carrasco).  
*Tetrastichus* sp. (Hym., Eulophidae).  
 Montevideo.  
*Timberlaxia* sp. nov. (Hym., Encyrtidae).  
 Montevideo (Carrasco).  
*Zophodia* sp. aff. *goyensis* Rag. (Lep.,  
 Phycitidae). (Predator-Inquilino).  
 Montevideo.  
 Chermidae sp.  
*Ablerus molestus* Blnchd. (Hym.,  
 Aphelinidae). "Males appear to be  
 hyperparasites of psyllid pupa via  
*Anagyrus chilensis* Brèthes." (Parker,  
 Berry & Silveira). Montevideo  
 (Carrasco).  
*Aenasius punctatus* Comp.  
 (Hym., Encyrtidae). Montevideo.  
*Anagyrus chilensis* Brèthes  
 (Hym., Encyrtidae). Montevideo.  
*Psyllaephagus* sp. aff. *arbuticola* G. & W.  
 (Hym., Encyrtidae). Montevideo.  
*Thysanus* sp. (Hym., Encyrtidae).  
 "Appear to be hyperparasites on psyllid  
 via chalcid, probably *Anagyrus chilensis*  
 Brèthes." (Parker, Berry & Silveira).  
 Montevideo (Carrasco).  
*Chrysomphalus dictyospermi* Morgan  
 (Diaspididae)  
*Thysanus* sp. (Hym., Encyrtidae).  
 Soriano (Mercedes).  
*Chrysomphalus* sp. aff. *pauлистus* Hemp.  
 (Diaspididae)  
*Tysanus* sp. (Hym., Encyrtidae).  
 Montevideo.  
*Chrysomphalus* sp. (Diaspididae)  
*Lindorus lophantae* (Blaisd.) (Col.,  
 Coccinellidae). Montevideo.  
 Coccoidea pl. sp.  
*Hyperaspis festiva* Muls.  
 (Col., Coccinellidae). Montevideo.  
*Psyllobora picta* Germ.  
 (Col., Coccinellidae). Montevideo.  
*Coccus perlatus* (Ckll.) (Coccidae)  
*Coccophagus caridei* (Brèthes) (Hym.,  
 Aphelinidae). Colonia (Colonia Suiza).  
*Coccophagus* sp. (Hym., Aphelinidae).  
 Colonia.  
*Cybocephalus* sp. (Col., Cybocephalidae).  
 Salto.  
*Hyperaspis connectens* Thunbg.  
 (Col., Coccinellidae). Salto.  
*Picnocephalus argentinus* Brèthes  
 (Col., Nitidulidae). Montevideo, Rivera.  
*Tetrastichus* sp. (Hym., Eulophidae).  
 Montevideo.  
*Zatropis* sp. (Hym., Pteromalidae).  
 Colonia.  
 Diaspididae sp.  
*Aphidoletes* sp. (Dip., Cecidomyiidae).  
 Montevideo.  
*Aphytis diaspidis* How. (Hym.,  
 Aphelinidae). Montevideo.  
*Aspidiotiphagus citrinus* (Cwfd.)  
 (Hym., Aphelinidae). Montevideo.  
*Thysanus merceti* Mal. (Hym., Encyrtidae).  
 Montevideo (Carrasco).  
*Diaspis echinocacti* (Bouché) (Diaspididae)  
*Aphytis diaspidis* How. (Hym.,  
 Aphelinidae). Montevideo.  
*Aspidiotiphagus citrinus* (Cwfd.) (Hym.,  
 Aphelinidae). Montevideo.  
*Scymnus* sp. (Col., Coccinellidae).  
 Montevideo.  
*Eriosoma lanigerum* Hausm. (Eriosomatidae)  
*Aphelinus mali* Hald. (Hym., Aphelinidae).  
 Canelones, Montevideo.  
*Eulecanium perinflatum* (Ckll.) (Coccidae)  
*Ablerus molestus* Blnchd. (Hym.,  
 Aphelinidae). Canelones (Pando).  
*Aphycus* sp. (Hym., Encyrtidae). Colonia  
 (Colonia Suiza), Montevideo.  
*Aneristus coccidis* Blnchd. (Hym.,  
 Aphelinidae). Colonia (Colonia Suiza),  
 San José.  
*Aneristus* sp. (Hym., Aphelinidae).  
 Canelones (Pando).  
*Coccidoxenus* sp. nov. (Hym., Encyrtidae).  
 Colonia (Colonia Suiza).  
*Coccophagus caridei* (Brèthes) (Hym.,  
 Aphelinidae). Colonia (Colonia Suiza),  
 Montevideo.  
*Eupelmus coccidivorus* Gah. (Hym.,  
 Eupelmidae). Canelones (Pando).  
*Gahaniella saissetiae* Timb. (Hym.,  
 Encyrtidae). Canelones (Pando).  
*Picnocephalus argentinus* Brèthes  
 (Col., Nitidulidae). Colonia.  
*Tetrastichus* sp. (Hym., Eulophidae).  
 Colonia (Colonia Suiza).  
*Hemiberlesia rapax* (Comstock) (Diaspididae)  
*Ablerus molestus* Blnchd. (Hym.,  
 Aphelinidae). Montevideo.  
*Ablerus peruvianus* Gir. (Hym.,  
 Aphelinidae). Montevideo (Carrasco).  
*Coccidencyrtus* sp. (Hym., Encyrtidae).  
 Montevideo (Carrasco).  
*Coccidophilus* sp. (Col., Discolomidae).  
 Montevideo.  
*Coccophagus caridei* (Brèthes) (Hym.,  
 Aphelinidae). Montevideo.  
*Coccophagus scutellaris* Dalm. (Hym.,  
 Aphelinidae). Montevideo.  
*Coccophagus* sp. (Hym., Aphelinidae).  
 Montevideo.  
*Enargopelte* sp. nov. (Hym., Pteromalidae).  
 Montevideo.



## HOMOPTERA (cont.)

- Eupelmus coccidivorus* Gah. (Hym., Eupelmidae). Montevideo.  
*Gahaniella saissetiae* Timb. (Hym., Encyrtidae). Montevideo.  
*Prospaltella* sp. (Hym., Aphelinidae). Montevideo.  
*Tetrastichus* sp. (Hym., Eulophidae). Montevideo.  
*Thysanus merceti* Mal. (Hym., Encyrtidae). Montevideo.  
*Timberlaxia* sp. (Hym., Encyrtidae). Montevideo (Carrasco).
- Homoptera sp.
- Gonatocerus* sp. (Hym., Mymaridae). Canelones (Pando).  
*Icerya purchasi* (Maskell) (Monophlebidae)  
*Megaselia* sp. (Dip., Phoridae). Canelones.  
*Rodolia cardinalis* (Muls.) (Col., Coccinellidae). Montevideo.  
*Syneura cocciphila* Coquillet (Dip., Phoridae). Canelones.  
*Icerya* sp. (Monophlebidae)  
*Brethesiella abnormicornis* Gir. (Hym., Encyrtidae). Rocha.
- Jassidae sp.
- Walzia* sp. (Acar., Anystidae). Colonia.  
*Kronides incumbens* (Germ.) (Membracidae)  
*Ufens* sp. (Hym., Trichogrammatidae). Florida (Casupá).  
*Lecanium hesperidum* (L.) (Coccidae)  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Canelones (Pando).  
*Lepidosaphes* sp. (Diaspididae)  
*Cales noacki* How. (Hym., Aphelinidae). Montevideo.  
*Prospaltella* sp. (Hym., Aphelinidae). Montevideo.  
*Macrosiphum solanifolii* (Ashm.) (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Florida.  
*Diaeretus plesiorapae* Blnchd. (Hym., Aphidiidae). Montevideo.  
*Myzus persicae* (Sulz.) (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Colonia, Florida, Montevideo.  
*Diaeretus plesiorapae* Blnchd. (Hym., Aphidiidae). Colonia, Montevideo.  
*Neocoelostoma* sp. (Monophlebidae)  
*Anystis* sp. (Acar., Anystidae). Montevideo.  
*Cerchysius* sp. (Hym., Encyrtidae). Montevideo.  
*Colastes* sp. (Hym., Braconidae). Montevideo.  
*Eudibazon* sp. (Hym., Braconidae). Montevideo.  
*Fidiobia* sp. (Hym., Platygasteridae). Montevideo.  
*Perilampus* sp. (Hym., Perilampidae). Montevideo.  
*Pristomerus* sp. (Hym., Ichneumonidae). Montevideo.  
*Neocoelostoma xerophila* Hemp. (Monophlebidae)  
*Catorama* sp. (Col., Anobiidae). Canelones.  
*Eupelmus coccidivorus* Gah. (Hym., Eupelmidae). Montevideo.
- Exoplectra* sp. (Col., Coccinellidae). Montevideo.  
*Hyperaspis* sp. (Col., Coccinellidae). Montevideo.  
*Laetilia* sp. (o gen. aff.) (Lep., Phycitidae). (Inquilino-Predator). Montevideo.  
*Syneura cocciphila* (Coquillet) (Dip., Phoridae). Montevideo.  
*Phenacoccus* sp. aff. *helianthi* (Ckll.) (Eriococcidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Montevideo.  
*Aenasius hyettus* Wlk. (Hym., Encyrtidae). Montevideo.  
*Leucopis* sp. aff. *nigricornis* Egger. (Dip., Chamaemyiidae). Montevideo.  
*Paranusia* sp. (Hym., Encyrtidae). Montevideo.  
*Stemmatosteres apterus* Timb. (Hym., Encyrtidae). Montevideo.  
*Thysanus* sp. nov. (Hym., Encyrtidae). Montevideo.  
*Phenacoccus* sp. (Eriococcidae).  
*Paranusia* sp. (Hym., Encyrtidae). Montevideo.  
*Stemmatosteres apterus* Timb. (Hym., Encyrtidae). Montevideo.  
*Pseudaulacaspis pentagona* (Targ.-Tozz.) (Diaspididae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). San José.  
*Ablerus peruvianus* Gir. (Hym., Aphelinidae). Montevideo (Melilla), San José.  
*Lindorus lophantae* (Blaisd.) (Col., Coccinellidae). Montevideo.  
*Prospaltella berlesei* (How.) (Hym., Aphelinidae). Canelones, Montevideo, San José.  
*Thysanus bifasciatus* Ashm. (Hym., Encyrtidae). Montevideo (Melilla).  
*Pseudaulacaspis* sp. prox. (Diaspididae)  
*Prospaltella* sp. (Hym., Aphelinidae). Montevideo (Melilla).  
*Pseudococcus* sp. (Eriococcidae)  
*Acerophagus* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Aenasius* sp. (Hym., Encyrtidae). Montevideo (Carrasco).  
*Brethesiella abnormicornis* Gir. (Hym., Encyrtidae). Rocha.  
*Psylla pyricola* Först. (Chermidae)  
*Chrysopa lanata* Banks (Neur., Chrysopidae). Montevideo.  
*Quadraspidotus perniciosus* (Comst.) (Diaspididae)  
*Chilocorus bipustulatus* L. (Col., Coccinellidae). Montevideo.  
*Chilocorus stigma* Say (Col., Coccinellidae). Montevideo.  
*Coccidophilus* sp. (Col., Discolomidae). Rivera, Tacuarembó.  
*Lindorus lophantae* (Blaisd.) (Col., Coccinellidae). Montevideo.  
*Rhopalosiphum maidis* Fitch. (Aphididae)  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Montevideo.  
*Metasyrphus* sp. (Dip., Syrphidae). San José.  
*Saissetia hemisphaerica* (Targ.) (Coccidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Montevideo.



## HOMOPTERA (cont.)

- Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Lecaniobius capitatus* Gah. (Hym., Eupelmidae). Salto.  
*Saissetia oleae* (Bern.) (Coccidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Salto.  
*Ablerus* sp. (Hym., Aphelinidae). Salto.  
*Coccophagus caridei* (Brèthes) (Hym., Aphelinidae). Montevideo.  
*Eupelmus coccidivorus* Gah. (Hym., Eupelmidae). Salto.  
*Lecaniobius capitatus* Gah. (Hym., Eupelmidae). Salto.  
*Lecaniobius utilis* Comp. (Hym., Eupelmidae). Salto.  
*Tetrastichus zemani* Brèthes (Hym., Eulophidae). Montevideo.  
*Saissetia silvestrii* Leon. (Coccidae)  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Paysandú.  
*Coccophagus saissetiae* Gah. (Hym., Aphelinidae). Paysandú.  
*Schizaphis graminum* (Rond.) (Aphididae)  
*Allograpta exotica* (Wied.) (Dip., Syrphidae). Montevideo.  
*Alloxysta* sp. (Hym., Cynipidae).  
 "Ex material, probably secondary"  
 (Parker, Berry & Silveira). Colonia.  
*Aphelinus mali* Hald. (Hym., Aphelinidae). Colonia.  
*Aphidencyrthus* sp. (Hym., Encyrtidae). San José.  
*Aphidius platensis* Brèthes (Hym., Aphidiidae). Uruguay.  
*Asaphes* sp. (Hym., Pteromalidae).  
 Probable parásito secundario, via  
*Aphidius platensis* Brèthes. San José.  
*Chrysopa lanata* Banks (Neur., Chrysopidae). Montevideo.  
*Coccinella ancoralis* (Germ.) (Col., Coccinellidae). Montevideo.  
*Cycloneda sanguinea* (L.) (Col., Coccinellidae). Montevideo.  
*Eriopis connexa* (Germ.) (Col., Coccinellidae). Montevideo.  
*Horismenus* sp. (Hym., Eulophidae). San José.  
*Metasyrphus* sp. (Dip., Syrphidae). San José.  
*Pachyneuron siphonophorae* Ashm. (Hym., Pteromalidae). San José.  
*Toxoptera aurantii* (Fons.) (Aphididae)  
*Alloxysta* sp. (Hym., Cynipidae).  
 "Probably hyperparasite of *T. aurantii* via  
 some *Aphidius*" (Parker, Berry & Silveira).

## HYMENOPTERA

- Anagyrus chilensis* Brèthes (Encyrtidae)  
*Thysanus* sp. (Hym., Encyrtidae). Montevideo.  
*Apanteles* sp. (Braconidae)  
*Eupteromalus* sp. (Hym., Pteromalidae). Soriano (Mercedes).  
*Aphidius platensis* Brèthes (Aphidiidae)  
*Alloxysta* sp. (Hym., Cynipidae). Colonia.  
*Aphidencyrthus* sp. (Hym., Encyrtidae). San José.  
*Asaphes* sp. (Hym., Pteromalidae). San José.  
*Charips grioti* De Santis (Hym., Charipidae). Colonia.  
*Horismenus* sp. (Hym., Eulophidae). San José.  
*Apis mellifera* L. (Apidae)  
*Mallophora ruficauda* Wied. (Dip., Asilidae). Montevideo.  
*Bassus* sp. (Braconidae)  
*Tetrastichus chapadae* Ashm. (Hym., Eulophidae). Colonia (Colonia Suiza), Montevideo.  
*Chalcidoidea* sp.  
*Ablerus molestus* Blnchd. (Hym., Aphelinidae). Montevideo (Carrasco).  
*Diaeretus plesiorapae* Blnchd. (Aphidiidae)  
*Charips* sp. (Hym., Charipidae). Montevideo.  
*Diaeretus rapae* (Curt.) (Aphidiidae)  
*Charips brassicae* Ashm. (Hym., Charipidae). Montevideo.  
Formicidae pl. sp.  
*Ameromyia* pl. sp. (Neur., Myrmeleontidae). Montevideo.  
Ichneumonidae sp.  
*Spilochalcis chapadae* Ashm. (Hym., Chalcididae). Paysandú, Soriano (Mercedes).  
Microgastrinae sp. (Braconidae)  
*Haltichella* sp. (Hym., Chalcididae). San José.  
*Neocryptopteryx orientalis* Blnchd. (Ichneumonidae)  
*Holcopeltomorpha* sp. (Hym., Eulophidae). Montevideo (Sayago).  
*Tetrastichus carbonelli* Blnchd. (Hym., Eulophidae). Montevideo (Sayago).  
*Tetrastichus* sp. (Hym., Eulophidae). Montevideo (Sayago).  
*Neonortoniella plusiae* Blnchd. (Ichneumonidae)  
*Eupelmus elegans* Blnchd. (Hym., Eupelmidae). Durazno (Blanquillo).  
*Spilochalcis ruffinellii* Blnchd. (Hym., Chalcididae). Durazno (Blanquillo).  
*Rogas nigriceps* Brèthes (Braconidae)  
*Spilochalcis ruffinellii* Blnchd. (Hym., Chalcididae). Durazno (Blanquillo).

## ISOPTERA

- Nasutitermes* sp. (Termitidae)  
*Cryptocheilis* sp. (Hym., Pompilidae). Montevideo.

## LEPIDOPTERA

- Aciptilia* sp. (Pterophoridae)  
*Horogenes* sp. (Hym., Ichneumonidae).  
 Canelones.  
*Alabama argillacea* (Hbn.) (Noctuidae)  
*Patelloa* sp. (Dip., Tachinidae). Uruguay.  
*Antarctia fusca* (Wlk.) (Arctiidae)  
*Apanteles* sp. (Hym., Braconidae).  
 Montevideo.  
*Anticarsia gemmatilis* Hbn. (Noctuidae)  
*Archytas incerta* (Macq.) (Dip.,  
 Tachinidae). Rivera.  
*Artiidae* sp.  
*Achaetoneura aletiae* (Riley) (Dip.,  
 Tachinidae). Montevideo.  
*Apanteles subcristatus* Blnchd. (Hym.,  
 Braconidae). Treinta y Tres (Laguna  
 Merín).  
*Argyrotaenia* sp. aff. *citharexylana* (Zell.)  
 (Tortricidae)  
*Apanteles* sp. nov. (Hym., Braconidae).  
 Montevideo.  
*Campoplex bonariensis* Schr. (Hym.,  
 Ichneumonidae). Montevideo.  
*Microbracon* sp. (Hym., Braconidae).  
 Montevideo.  
*Cactoblastis cactorum* Berg (Phycitidae)  
*Apanteles alexanderi* Brèthes (Hym.,  
 Braconidae). Canelones (Pando).  
*Colcophoridae* sp.  
*Spilochalcis chapadae* Ashm. (Hym.,  
 Chalcididae). Montevideo.  
*Colias lesbia pyrrhothea* Hbn. (Pieridae)  
*Apanteles glomeratus* L. (Hym.,  
 Braconidae). Montevideo.  
*Euphorocera floridensis* Tns. (Dip.,  
 Tachinidae). Montevideo.  
*Crambus* sp. aff. *faunellus* Schaus (Crambidae)  
*Prosopochaeta* sp. (Dip., Tachinidae).  
 Montevideo.  
*Diaphania hyalinata* (L.) (Pyraustidae)  
*Meteorus* sp. (Hym., Braconidae). San José.  
*Diatraea saccharalis* (Fabr.) (Crambidae)  
*Bassus stigmaterus* Cress. (Hym.,  
 Braconidae). San José.  
*Calliephialtes* sp. (Hym., Ichneumonidae).  
 San José.  
*Ipobracon amabilis* (Brèthes) (Hym.,  
 Braconidae). San José.  
*Ipobracon* sp. (Hym., Braconidae).  
 Durazno (Blanquillo).  
*Ecpantheria indecisa* Wlk. (Arctiidae)  
*Euanisia mesa-carrioni* Blnchd. (Dip.,  
 Tachinidae). Montevideo.  
*Plagiotachina caridei* (Brèthes) (Dip.,  
 Tachinidae). Soriano.  
*Plagiotachina haywardi* Blnchd. (Dip.,  
 Tachinidae). Soriano.  
*Pimpla videonis* (Morl.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Ephestia kühniella* Zell. (Phycitidae)  
*Idechthis canescens* (Grav.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Eulia sphaleropa* (Meyrick) (Tortricidae)  
*Brachymeria pseudovata* Blnchd. (Hym.,  
 Chalcididae). Canelones, Montevideo.  
*Euptoieta claudia hortensia* (Blanch.)  
 (Nymphalidae)  
*Euphorocera floridensis* Tns. (Dip.,  
 Tachinidae). Colonia, San José.
- Faronta albilinea* (Hbn.) (Noctuidae)  
*Apanteles* sp. nov. (Hym., Braconidae).  
 Canelones, Florida, Montevideo,  
 San José.  
*Campoletis argentifrons* (Cress.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Campoletis* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Casinaria* sp. (Hym., Ichneumonidae).  
 Maldonado, Montevideo.  
*Crocota* sp. nov. aff. *geniculata* (Deg.)  
 (Dip., Tachinidae). Canelones.  
*Enicospilus merdarius* (Grav.) (Hym.,  
 Ichneumonidae). Montevideo.  
*Euphorocera floridensis* Tns. (Dip.,  
 Tachinidae). Colonia, Montevideo,  
 San José.  
*Hyposoter* sp. (Hym., Ichneumonidae).  
 Canelones, Florida (Casupá), San José.  
*Microplitis* sp. nov. (Hym., Braconidae).  
 Colonia.  
*Rogas* sp. (Hym., Braconidae). Canelones,  
 Montevideo, San José.  
*Sagaritis provancheri* (D.T.) (Hym.,  
 Ichneumonidae). Florida, Montevideo,  
 San José.  
*Siphocrocota* sp. nov. (Dip., Tachinidae).  
 Canelones, Río Negro.  
*Gnorimoschema operculella* (Zell.)  
 (Gelechiidae)  
*Arrenoclavus koehleri* (Blnchd.) (Hym.,  
 Encyrtidae). Colonia (Estanzuela).  
*Gnorimoschema* sp. (Gelechiidae)  
*Amobia* sp. (Dip., Tachinidae). Canelones.  
*Apanteles* sp. (Hym., Braconidae).  
 Montevideo.  
*Bassus* sp. (Hym., Braconidae). Canelones,  
 Montevideo.  
*Brachymeria* sp. aff. *hammari* Cwfd.  
 (Hym., Chalcididae). Montevideo.  
*Copidosoma* sp. (Hym., Encyrtidae).  
 Montevideo.  
*Monodontomerus* sp. (Hym., Torymidae).  
 Canelones (Pando).  
*Orgilus* sp. (Hym., Braconidae).  
 Montevideo.  
*Spilochalcis chapadae* Ashm. (Hym.,  
 Chalcididae). Montevideo.  
*Grapholita molesta* (Busk) (Olethreutidae)  
*Dibrachys cavus* Wlk. (Hym.,  
 Pteromalidae). Montevideo.  
*Halisidota* sp. (Arctiidae)  
*Podisus nigrolimbatus* Spin. (Hem.,  
 Pentatomidae). Montevideo.  
*Heliothis armigera* (Hbn.) (Noctuidae)  
*Actinoplusia koehleri* Blnchd. (Dip.,  
 Tachinidae). Canelones, Colonia.  
*Amblyteles* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Calosoma retusum* Fabr. (Col., Carabidae).  
 Colonia.  
*Campoletis argentifrons* (Cress.) (Hym.,  
 Ichneumonidae). Colonia (Colonia  
 Suiza).  
*Hyposoter* sp. (Hym., Ichneumonidae).  
 Colonia, Florida (Casupá).  
*Netelia* sp. (Hym., Ichneumonidae).  
 Colonia.  
*Ophion ancyloneura* Cam. (Hym.,  
 Ichneumonidae). Montevideo.  
*Paniscus* sp. (Hym., Ichneumonidae).  
 Florida (Casupá), Montevideo.

## LEPIDOPTERA (cont.)

- Plagiotachina floridensis* Tns. (Dip., Tachinidae). Durazno.  
*Sagaritis provancheri* (D.T.) (Hym., Ichneumonidae). Florida, Montevideo, San José.  
*Herse cingulata* Fabr. (Sphingidae)  
*Microplitis ayerzai* Brèthes (Hym., Braconidae). Durazno (Blanquillo).  
*Homoeosoma nebulellum* (Hbn.) (Phycitidae)  
*Agathis* sp. (Hym., Braconidae).  
 Artigas (Bella Unión).  
*Eiphosoma variegatum* Brèthes (Hym., Ichneumonidae). Artigas (Bella Unión).  
*Hylephila* sp. (Hesperiidae)  
*Saropogon* sp. (Dip., Asilidae). San José.  
*Laetilia* sp. (Phycitidae)  
*Apanteles* sp. nov. aff. *alexanderi* Brèthes (Hym., Braconidae). Montevideo.  
*Laphygma frugiperda* (S. & A.) (Noctuidae)  
*Achaetoneura* sp. (Dip., Tachinidae).  
 Cerro Largo, Montevideo.  
*Apanteles marginiventris* (Cress.) (Hym., Braconidae). Río Negro (Colonia Inglaterra).  
*Archytas incerta* (Macq.) (Dip., Tachinidae). Montevideo, R. Negro.  
*Atrometus tricolor* Szepi. (Hym., Ichneumonidae). San José.  
*Atrometus* sp. (prob. *reticulatus* End.) (Hym., Ichneumonidae). San José.  
*Calosoma retusum* Fabr. (Col., Carabidae).  
 Colonia.  
*Campoletis argentifrons* (Cress.) (Hym., Ichneumonidae). Montevideo.  
*Chelonus texanus* Cress. (Hym., Braconidae). Río Negro, San José.  
*Hyposoter* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Incamiya chilensis* Ald. (Dip., Tachinidae).  
 San José.  
*Mermis* sp. (Nematoda, Mermittidae).  
 Cerro Largo.  
*Microplitis* sp. (Hym., Braconidae).  
 Montevideo.  
*Ophion ancyloneura* Cam. (Hym., Ichneumonidae). Montevideo, Río Negro (Young), San José.  
*Parasetigena* sp. (Dip., Tachinidae).  
 Montevideo.  
*Patelloa* sp. (Dip., Tachinidae).  
 Cerro Largo.  
*Pseudoarchytopsis* sp. (Dip., Tachinidae).  
 San José.  
*Sagaritis provancheri* (D.T.) (Hym., Ichneumonidae). Colonia, San José.  
*Voria ruralis* (Fall.) (Dip., Tachinidae).  
 Canelones, Cerro Largo, Río Negro.
- Lepidoptera pl. sp.  
*Alcaeorhynchus grandis* Dall. (Hem., Pentatomidae). Montevideo.  
*Oplomus cruentus* Burm. (Hem., Pentatomidae). Montevideo.  
*Podisus nigrispinus* Dall. (Hem., Pentatomidae). Montevideo.  
*Pyemotes ventricosus* (Newport) (Acar., Tarsonemidae). Montevideo.
- Lepidoptera sp.  
*Amblyteles* sp. (Hym., Ichneumonidae).  
 San José.
- Angitia* sp. (Hym., Ichneumonidae).  
 Canelones.  
*Apanteles* sp. (Braconidae). Salto.  
*Calliephialtes* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Meteorius* sp. (Hym., Braconidae).  
 Montevideo.  
*Nepocarcellia falva* Tns. (Dip., Tachinidae). Tacuarembó.  
*Mallocephala deserticola* Berg (Arctiidae)  
*Achaetoneura* sp. (Dip., Tachinidae).  
 Colonia.  
*Euanisia mesa-carrioni* Blnchd. (Dip., Tachinidae). Montevideo.  
*Rogas* sp. (Hym., Braconidae). Colonia.  
*Zygofrontina* sp. (Dip., Tachinidae).  
 Colonia, San José.  
*Megalopyge urens* Berg (Megalopygidae)  
*Neocryptopteryx orientalis* Blnchd. (Hym., Ichneumonidae). Montevideo.  
*Mimallo* sp. (Mimallonidae)  
*Brachymeria* sp. (Hym., Chalcididae).  
 Montevideo.
- Noctuidae pl. sp.  
*Ophion biangularis* Tasch. (Hym., Ichneumonidae). Montevideo.  
*Oiketicus kirbyi* (Guild.) (Psychidae)  
*Ipobracon sublucens* Blnchd. (Hym., Braconidae). Canelones (Pando),  
 Montevideo.  
*Perissocentrus caridei* Brèthes. (Hym., Torymidae). Montevideo.  
*Psychidosmicra brasiliensis* (Brèthes)  
 Hym., Chalcididae). Montevideo  
 (Sayago).  
*Tetrastichus pseudoeceticola* (Blnchd.)  
 (Hym., Eulophidae). Montevideo.  
*Oiketicus* sp. aff. *geyeri* (Berg) (Psychidae)  
*Perissocentrus argentinae* Cwfd. (Hym., Torymidae). Canelones (Pando).  
*Tetrastichus isis* Brèthes (Hym., Eulophidae). Canelones (Pando).  
*Papilio thoas brasiliensis* R. & J.  
 (Papilionidae)  
*Pteromalus caridei* Brèthes. (Hym., Pteromalidae). Montevideo.  
*Peridroma margaritosa* (Haw.) (Noctuidae)  
*Amblyteles* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Apanteles bourquini* Blnchd. (Hym., Braconidae). Montevideo.  
*Apanteles elegans* Blanchd. (Hym., Braconidae). Montevideo.  
*Copidosoma* sp. aff. *truncatellum* (Dalm.)  
 (Hym., Encyrtidae). Montevideo.
- Pieridae sp.  
*Pteromalus puparum* (L.) (Hym., Pteromalidae). San José.  
*Plodia interpunctella* Hbn. (Phycitidae)  
*Idechthis canescens* Grav. (Hym., Ichneumonidae). Montevideo.  
*Plusia nu* (Gn.) (Noctuidae)  
*Achaetoneura* sp. (Dip., Tachinidae).  
 Cerro Largo.  
*Acladra kinbergi* Stal (Hem., Pentatomidae). Durazno (Blanquillo).  
*Apanteles* sp. nov. (Hym., Braconidae).  
 Cerro Largo.

## LEPIDOPTERA (cont.)

- Brachymeria ovata* Say (Hym., Chalcididae). Cerro Largo, Durazno (Blanquillo).  
*Calosoma retusum* Fabr. (Col., Carabidae). Cerro Largo, Colonia, Durazno, Montevideo, Río Negro, Salto.  
*Casinaria* sp. (Hym., Ichneumonidae). Cerro Largo, Florida (Casupá).  
*Copidosoma truncatellum* Dalm. (Hym., Encyrtidae). Cerro Largo, Soriano.  
*Enicospilus* sp. (Hym., Ichneumonidae). Cerro Largo.  
*Euplectrus insularis* How. (Hym., Eulophidae). Cerro Largo, Montevideo.  
*Hyposoter* sp. (Hym., Ichneumonidae). Montevideo.  
*Litomastix brethesi* Blnchd. (Hym., Encyrtidae). Durazno (Blanquillo), Artigas, Salto.  
*Microplitis* sp. nov. (Hym., Braconidae). Montevideo.  
*Neonortoniella plusiae* Blnchd. (Hym., Ichneumonidae). Durazno (Blanquillo).  
*Oplomus cruentus* Burm. (Hem., Pentatomidae). Durazno (Blanquillo).  
*Patelloa* sp. (Dip., Tachinidae). Cerro Largo.  
*Patelloapsis rusti* (Ald.) (Dip., Tachinidae). Cerro Largo.  
*Podisus aenescens* Stal (Hem., Pentatomidae). Durazno (Blanquillo).  
*Podisus australis* Berg (Hem., Pentatomidae). Durazno (Blanquillo).  
*Podisus nigrispinus* Dall. (Hem., Pentatomidae). Durazno (Blanquillo).  
*Pterostichus striatulus* Fabr. (Col., Carabidae). Colonia.  
*Rogas nigriceps* Brèthes (Hym., Braconidae). Cerro Largo, Durazno (Blanquillo), Colonia (Colonia Suiza).  
*Voria ayerzai* (Brèthes) (Dip., Tachinidae). Durazno (Blanquillo).  
*Voria brasiliiana* Tns. (Dip., Tachinidae). Montevideo.  
*Voria ruralis* (Fall.) (Dip., Tachinidae). Canelones, Río Negro.  
*Plutella maculipennis* (Curt.) (Plutellidae).  
*Apanteles* sp. (Hym., Braconidae). Montevideo.  
*Eulimneria leontinae* (Brèthes) (Hym., Ichneumonidae). Montevideo (Sayago).  
*Spilochalcis chapadae* Ashm. (Hym., Chalcididae). Montevideo.  
*Protoparce sexta paphus* Cram. (Sphingidae).  
*Microplitis ayerzai* Brèthes (Hym., Braconidae). Durazno (Blanquillo).  
*Protoparce* sp. (Sphingidae).  
*Apanteles paphi* Schrottky (Hym., Braconidae). Treinta y Tress.  
*Pseudaletia unipuncta* (Haw.) (Noctuidae).  
*Agrothereutes* sp. nov. (Hym., Ichneumonidae). Canelones.  
*Amblyteles* sp. (Hym., Ichneumonidae). Montevideo.  
*Amblytelini* sp. (Hym., Ichneumonidae). Montevideo.  
*Anthrax* sp. (Hym., Bombyliidae). Soriano.  
*Apanteles bourquini* Blnchd. (Hym., Braconidae). Montevideo (Sayago), Colonia (Estanzuela).  
*Apanteles elegans* Blnchd. (Hym., Braconidae). Montevideo (Sayago).  
*Apanteles* sp. nov. (Hym., Braconidae). Canelones, Florida, Montevideo, San José (Rincón del Pino).  
*Aphriosphyria grioti* Blnchd. (Tachinidae). Cerro Largo.  
*Archytas incerta* (Macq.) (Dip., Tachinidae). Montevideo, Río Negro, San José, Soriano.  
*Calosoma argentinensis* Csiki (Col., Carabidae). Montevideo, Río Negro.  
*Calosoma retusum* Fabr. (Col., Carabidae). San José.  
*Campoletis argentifrons* (Cress.) (Hym., Ichneumonidae). Colonia.  
*Campoletis* sp. (Hym., Ichneumonidae). Florida.  
*Campoplex fugitivus* Holliday (Hym., Ichneumonidae). Florida.  
*Cryptus melanostigma* Br. (Hym., Ichneumonidae). Montevideo, Soriano (Mercedes).  
*Enicospilus merdarius* (Grav.) (Hym., Ichneumonidae). Soriano (Mercedes).  
*Enicospilus* sp. (Hym., Ichneumonidae). Montevideo.  
*Euplectrus platyhypenae* How. (Hym., Eulophidae). Colonia.  
*Horogenes* sp. (Hym., Ichneumonidae). Montevideo.  
*Hyposoter* sp. (Hym., Ichneumonidae). Montevideo, San José.  
*Microplitis* sp. nov. (Hym., Braconidae). Colonia, Florida, Montevideo.  
*Netelia* sp. (Hym., Ichneumonidae). Soriano (Mercedes).  
*Ophion ancyloneura* Cam. (Hym., Ichneumonidae). Colonia, Soriano (Mercedes).  
*Peleteria robusta* (Wied.) (Dip., Tachinidae). Colonia.  
*Phorocera* sp. (Dip., Tachinidae). San José.  
*Plagiotachina* sp. nov. (Dip., Tachinidae). Montevideo, Río Negro, San José, Soriano.  
*Rogas* sp. nov. (Hym., Braconidae). Montevideo, San José.  
*Sagaritis* sp. (Hym., Ichneumonidae). Florida, Montevideo.  
*Sagaritis provancheri* (D.T.) (Hym., Ichneumonidae). Montevideo.  
*Siphocrocuta* sp. nov. (Dip., Tachinidae). Canelones, Río Negro.  
*Trogomorpha* sp. (Hym., Ichneumonidae). Montevideo.  
 Pyralididae pl. sp.  
*Microbracon hebetor* (Say) (Hym., Braconidae). Montevideo.  
 Pyralididae sp.  
*Trichogramma minutum* Riley (Trichogrammatidae). Montevideo.  
*Sitotroga cerealella* (Ol.) (Gelechiidae).  
*Habrocytus lineatiporus* Blnchd. (Hym., Pteromalidae). Montevideo.  
*Tatochila autodice* (Hbn.) (Pieridae).  
*Apanteles glomeratus* L. (Hym., Braconidae). Montevideo.  
*Apanteles williamsoni* Blnchd. (Hym., Braconidae). Durazno (Blanquillo).

## LEPIDOPTERA (cont.)

- Tecia* sp. (Gelechiidae)  
*Calliephialtes* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Pimploterus* sp. (Hym., Ichneumonidae).  
 Montevideo.  
*Telphusa* sp. (Gelechiidae)  
*Apanteles* sp. (Hym., Braconidae). Florida.  
*Microgaster* sp. (Hym., Braconidae).  
 Florida.

- Titya proxima* Burm. (Lasiocampidae)  
*Apanteles lizeri* Blnchd. (Hym.,  
 Braconidae). Montevideo.  
*Vanessa virginiensis rubia* (Stgr.)  
 (Nymphalidae)  
*Apanteles subcristatus* Blnchd. (Hym.,  
 Braconidae). Treinta y Tres (Laguna  
 Merín).

## MANTODEA

- Coptopteryx* sp. (Mantidae)  
*Sarcophaga* sp. nov. aff. *mantidophaga*  
 Blnchd. (Dip., Sarcophagidae).  
 Canelones.

- Mantidae sp.  
*Anastatus* sp. (Hym., Eupelmidae).  
 Canelones.

## ORTHOPTERA

- Acrididae pl. sp.  
*Coptopteryx gayi* (Blanch.) (Man.,  
 Mantidae). Artigas, Lavalleja, Rivera.  
*Dichroplus conspersus* Bruner (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Durazno, Florida.  
*Latrodectus mactans* Fabr. (Aran.,  
 Theridiidae). Durazno, Florida,  
 Tacuarembó.  
*Trombidiidae* sp. ign. (Acar.)  
 Lavalleja, Rivera, Tacuarembó.  
*Wixia grayi* (Blackwall) (Aran.,  
 Argiopidae). Durazno, Florida, Lavalleja.  
*Dichroplus pratensis* (Bruner) (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Durazno, Florida.  
*Coptopteryx claraziana* Sauss. (Man.,  
 Mantidae). Durazno.  
*Mermitidae* sp. (Nematoda).  
 Durazno.  
*Trombidiidae* sp. ign. (Acar.).  
 Durazno, Lavalleja, Tacuarembó.  
*Dichroplus* sp.  
*Neorhynchocephalus* sp. (Dip.,  
 Nemestrinidae). Durazno, Tacuarembó.  
*Protodexia australis* Blnchd. (Dip.,  
 Sarcophagidae). Durazno, Florida,  
 Flores, Tacuarembó.  
*Diponthus maculiferus* (Walker) (Acrididae)  
*Trombidiidae* sp. ign. (Acar.).  
 Lavalleja, Rivera, Tacuarembó.  
*Elaeochlora viridicata* (Serville) (Acrididae)  
*Protodexia crouzei* Blnchd. (Dip.,  
 Sarcophagidae). Tacuarembó.  
*Gryllotalpa* sp. (Gryllotalpidae)  
*Larra* sp. (Hym., Larridae). San José  
 (Libertad).  
*Orphulella punctata* (De Geer) (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Durazno, Florida.  
*Trombidiidae* sp. ign. (Acar.)  
 Lavalleja, Rivera, Tacuarembó.  
 Orthoptera sp.  
*Centrodora perkinsi* Waterston (Hym.,  
 Aphelinidae). Montevideo.  
*Chlorionini* sp. (Sphecidae).  
 Montevideo.  
*Parorphula graminea* Bruner (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Durazno, Florida.  
*Coptopteryx claraziana* Sauss. (Man.,  
 Mantidae). Durazno.  
*Trombidiidae* sp. ign. (Acar.)  
 Lavalleja, Rivera, Tacuarembó.

- Rhammatocerus pictus* (Bruner) (Acrididae)  
*Trombidiidae* sp. ign. (Acar.).  
 Lavalleja, Rivera, Tacuarembó.  
*Schistocerca cancellata* (Serv.) (Acrididae)  
*Acridiophaga caridei* (Brèthes) (Dip.,  
 Sarcophagidae). Durazno.  
*Epicauta adspersa* Klug (Col., Meloidae).  
 Uruguay.  
*Hexamermis acridiorum* Weyenb.  
 (Nemat., Mermitidae), Uruguay.  
*Hylemyia cilicrura* Rond. (Dip.,  
 Anthomyiidae). Uruguay.  
*Probellieria securifera* (Vill.) (Dip.,  
 Sarcophagidae). Uruguay.  
*Trox suberosus* Fabr. (Col.,  
 Scarabaeidae). Uruguay.  
*Scotussa* ? sp.  
*Centrodora perkinsi* Waterston (Hym.,  
 Aphelinidae). Colonia.  
*Scyllinops bruneri* (Rehn) (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Florida, Durazno.  
*Coptopteryx claraziana* Sauss. (Man.,  
 Mantidae). Durazno.  
*Latrodectus mactans* Fab. (Aran.,  
 Theridiidae). Durazno, Florida,  
 Tacuarembó.  
*Scelio* sp. (Hym., Scelionidae).  
 Tacuarembó.  
*Trombidiidae* sp. ign. (Acar.).  
 Lavalleja, Rivera, Tacuarembó.  
*Wixia grayi* (Blackwall) (Aran.,  
 Argiopidae). Durazno, Florida,  
 Lavalleja.  
*Scyllinops pallida* (Bruner) (Acrididae)  
*Coptopteryx argentina* (Burm.) (Man.,  
 Mantidae). Artigas, Durazno, Florida.  
*Coptopteryx claraziana* Sauss. (Man.,  
 Mantidae). Durazno.  
*Latrodectus mactans* Fabr. (Aran.,  
 Theridiidae). Durazno, Florida,  
 Tacuarembó.  
*Trombidiidae* sp. ign. (Acar.).  
 Lavalleja, Rivera, Tacuarembó.  
*Wixia grayi* (Blackwall) (Aran.,  
 Argiopidae). Durazno, Florida,  
 Lavalleja.  
*Scyllinops* pl. sp.  
*Epicauta adspersa* Klug (Col., Meloidae).  
 Tacuarembó.  
*Epicauta griseonigra* (Fairm.) (Col.,  
 Meloidae). Tacuarembó.  
*Staurorhectus longicornis* G. Tos (Acrididae)  
*Trombidiidae* sp. ign. (Acar.).  
 Lavalleja, Rivera, Tacuarembó.



## THYSANOPTERA

Thysanoptera sp.

*Chrysopa lanata* Banks (Neur.,  
Chrysopidae). Montevideo.

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Section  
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**INDEX**

	Pages
Recent Studies on the Role of Insects in the Cross-Pollination of Crops . . . . .	927-990
General Papers . . . . .	991-1112

*The following paper was presented at the Congress but is not included herein:*

Contributions to Corbicular Pollen Analysis

By JOHN A. KNIERIM

Michigan State University

East Lansing, Mich.

and

W. E. DUNHAM

Ohio State University

Columbus, Ohio

# Pollination Studies on Red Clover

By E. BRAUN, R. M. MACVICAR, D. R. GIBSON, and P. PANKIW  
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Ottawa, Ont.

## ABSTRACT<sup>1</sup>

*The pollinating effectiveness of honeybees and bumblebees on red clover is dependent upon many factors, such as, amount of bloom, corolla tube length, quantity and quality of the nectar, freedom of the crop from insect damage, pollen availability, competing crops, distance of colony or nesting sites from the field, flight conditions, density and/or dispersal of populations over the field.*

*The 1952 studies showed that no increase in seed yields accrued from the use of more than two colonies per acre. Pollinator dispersal studies (1954) carried out on a 12- and a 36-acre field indicated that on the smaller field honeybees and bumblebees were evenly distributed while bumblebee populations decreased significantly from the periphery of the larger field to its centre.*

*The quality and quantity of nectar varied widely within as well as between fields, but there was no correlation between honeybee density and nectar volume. Measurement of nectar volume in excised florets indicated that in only eight per cent was the level of nectar high enough to make it available to honeybees.*

*It was apparent, from pollen-trap collections, that individual colonies showed definite preferences for certain types of pollen over others.*

The complete text will be submitted to the Canadian Journal of Agricultural Science.





# Alfalfa Pollinators with Special Reference to Species Other Than Honey Bees

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Logan, Utah

## ABSTRACT

Honey bees and many species of wild bees are the principal alfalfa pollinators. Over one hundred species of wild pollinators have been reported in the U. S. alone. The importance of wild bees depends upon their abundance, pollinating efficiency, and the local pollinating efficiency of honey bees.

In general honey bees pollinate alfalfa more efficiently in the warmer, drier parts of the world. Consequently wild bees are relatively important in cool or humid areas such as Canada, the northern United States, and most parts of Europe. They are relatively unimportant in the southwestern United States and most of Australia.

Bumble bees (*Bombus*) and leaf-cutting bees (*Megachile*) contain most of the important pollinators in North America and Europe. However, one or more species of other genera may be equally or more important in certain regions. *Nomia melanderi* (the alkali bee) is the most important wild bee in the Intermountain Region of the United States. *Andrena wilkella* is one of the most valuable species in the Great Lakes region. *Melitta leporina* and *Eucera longicornis* are important in Scandinavia. In parts of central Europe and Turkey, *Rhophites canus* is reported as responsible for most of the alfalfa pollination.

Establishment of alfalfa pollinators in new areas is strongly recommended. Such establishment should be easy in the case of *Bombus* and megachilids, but may be difficult in the case of solitary ground-nesting species.

Measures useful for preservation, increase, and better utilization of wild bees are as follows: (1) Locate seed fields where pollinators are abundant. (2) Time the bloom for the period of their greatest abundance. (3) Limit acreage in bloom at one time. (4) Reduce competing sources of pollen and nectar during blooming period of the seed crop. (5) Provide spring and early summer bloom for build up of long-season species. (6) Where possible, provide nesting sites or conditions suitable for nesting. (7) Search for nesting sites and keep them unaltered. (8) Avoid chemical insect control during bloom. If bloom stage treatments are necessary, use materials least harmful to bees and apply only when bees are not on the field.

The subject of alfalfa pollination was reviewed recently by Bohart (1957). The present paper emphasizes the activities of alfalfa pollinators (especially the wild ones) rather than plant responses. Problems of conserving, increasing, and making better use of wild pollinators are also discussed.

## INSECTS OTHER THAN BEES

Alfalfa flowers are entered in several ways by various groups of insects. Thrips (principally *Frankliniella* spp.) enter the flowers bodily and reach the nectaries without tripping them or contacting the stigma. Besides taking some nectar, they rasp the floral tissues and cause a mottling of the petals. Their effect on pollination is therefore negligible or slightly harmful, depending upon their abundance. Moths and butterflies insert their long, slender tongues directly into the throat of the flowers without causing them to trip. From the standpoint of pollination they are merely nectar thieves, since they lower the attractiveness of the flowers to pollinating insects.

Pierids, nymphalids, lycaenids, and noctuids are the lepidopterous families most commonly attracted to alfalfa in Utah. Alfalfa butterflies (*Colias* spp.) are sometimes extremely abundant, especially in California. Noctuid moths of the genus *Autographa* sometimes become nearly as abundant in the evening. The effect such populations might have on the attractiveness of the flowers to pollinators has not been evaluated.

<sup>1</sup>In cooperation with Utah Agricultural Experiment Station.

Meloid beetles (*Epicauta*) visit alfalfa racemes to feed on the flowers. The meloids often feed on the petals until the restraining mechanism is destroyed, thus allowing the flowers to trip. If the beetle is contacted when a flower trips, cross-pollination may result. However, damage to the flowers caused by indiscriminant feeding probably outweighs the advantage of occasional cross-pollination.

Cantharid beetles of the genus *Chauliognathus* have elongated gelesae which enable them to reach the nectaries through the throat of the flower. Such entry frequently results in tripping. However, the tripping rate is slow since the beetles usually crawl from raceme to raceme and often remain nearly motionless for long periods. Furthermore, they much prefer certain composites to alfalfa. Nevertheless, they have been rated as valuable pollinators in Nebraska by Tysdal (1940). Since *Chauliognathus* larvae are predatory on aphids and other harmful insects, they can be regarded as beneficial in this stage also. The possibility of increasing cantharids for release in alfalfa fields has apparently never been investigated.

Sphecid wasps in the genera *Bembix*, *Steniolia*, *Stictiella*, *Microbembex*, *Bicyrtes*, and *Sphex* are frequent visitors to alfalfa in some of the more arid regions of Utah. However, it is only rarely that they make a strong attempt to reach the nectaries. After searching for several hours near Delta, I found two individuals of *Stictiella pulla* (Handlirsch) tripping flowers regularly and accumulating a wet lump of pollen on the clypeus. A single individual of *Bembix connexa* Fox was seen tripping flowers on another occasion.

Scoliid wasps of the genus *Campsomeris* are apparently the only non-apoid Hymenoptera that trip alfalfa flowers consistently. Linsley (1946) stated that *Campsomeris pilipes* Cresson near Blythe, California, frequently trips flowers with its feet. I have observed several individuals of the same species in southern Utah tripping flowers regularly by thrusting their faces directly into the flowers. Because of their size and strength, they were able to trip flowers and reach the nectar easily. Pollen accumulated principally on the mandibles, clypeus, and maxillae. Unfortunately, *C. pilipes* females are rarely common enough on alfalfa to be important pollinators. Besides their value as pollinators, *Campsomeris* wasps are important enemies of scarabaeid larvae.

## BEES

### KINDS OF BEES INVOLVED

Honey bees are the most abundant and widespread alfalfa pollinators. In areas where they collect alfalfa pollen they are usually also the most important pollinators. However, their efficiency decreases sharply as the percentage of pollen collectors decreases. In areas where honey bees rarely collect alfalfa pollen, one or more of the other species of bees present on the field may be more important. In general, honey bees are most valuable in hot, dry areas. Wild bees are valuable wherever they are found in reasonable numbers on the field, but their relative importance increases in cooler climates where honey bees are usually less efficient.

Several hundred species of bees in about thirty genera are found in alfalfa seed fields of various parts of the world (Bohart 1957). The genera of widespread importance are: *Apis* (*mellifera* L.), *Bombus* (many species), and *Megachile* (many species). The following genera are of considerable importance in more limited areas: *Melissodes* (many species in western U.S.), *Eucera* (*longicornis* L. in western Europe and several species in central Asia), *Tetralonia* (*edwardsii*) Cress. in Utah and Idaho and *tricincta* Eversm. in central Asia), *Florilegus* (*condignus* Cress. in Kansas and Nebraska), *Hemisia* (*rhodopus* (Ckll.) in Arizona and southern Utah), *Melitturga* (*clavicornis* Latr. in central Asia), *Anthophora* (*magnilabris* Fedt. in central Asia and *urbana* Cress. in Utah), *Xylocopa* (several species in southwestern U.S. and Israel), *Osmia* (*seclusa* Sandh. in Utah and Idaho), *Halictus* (several species in western U.S. and central Asia), *Nomia* (*melanderi* Ckll. in western U.S. and *diversipes* Latr. in central Asia), *Rophites* (*canus* Eversm. in central and eastern Europe), *Melitta* (*leporina* Panz. in Europe and western Asia), *Andrena* (several species in northern U.S. and central Asia), and *Calliopsis* (*andreniformis* Smith in Nebraska). The remaining genera appear to be of little importance except on rare occasions or in very limited areas. However, surveys in

other important alfalfa-seed areas, such as Argentina and Australia, will undoubtedly show the existence of other important pollinators than those indicated above.

#### NECTAR COLLECTORS VS. POLLEN COLLECTORS

An individual bee may take nectar or pollen or both from alfalfa. Usually when it takes both, one food material is obviously the primary objective and the other is more or less accidental. Whether the bees are seeking pollen or nectar is the principal determinant of the effectiveness of their visits in terms of pollination. The percentage of nectar or pollen collectors found on an alfalfa field depends principally upon (1) the species and sex of the bees, (2) the needs of the nest, (3) the relative amounts and attractiveness of competing sources of pollen and nectar, and (4) the condition and variety of the alfalfa.

Apparently, male bees<sup>2</sup> and parasitic bees visit flowers for nectar only. Females of some species of nonparasitic bees always visit alfalfa for pollen and others always visit it for nectar. Most species fall somewhere between these extremes. In Utah species of *Halictus*, *Lasioglossum*, *Nomia*, *Nomadopsis*, *Andrena*, and *Colletes* apparently visit alfalfa for pollen only. Most species of *Megachile*, *Osmia*, *Hoplitis* and *Anthidium* do likewise, but a few individuals of some species can usually be seen collecting nectar. It is harder to generalize about anthophorids and apids. Some *Melissodes* and *Tetralonia*, for example, nearly always collect pollen when they visit alfalfa, but many species of *Anthophora* and *Bombus* frequently collect nectar. Under most conditions, as most of us know, the honey bee more often collects nectar than pollen from alfalfa. In general, solitary bees are more likely to collect pollen than social bees because they have no need to store supplies of nectar. Among the solitary bees, those that feed their young with the driest pollen mixes are the ones that make the highest percentage of pollen-collecting trips. Some bees collect little or no alfalfa pollen simply because their pollen host range does not normally include alfalfa, even though their nectar host range does. In Utah such bees include *Anthophora bomboidea neomexicana* Ckll., *A. pacifica* Cress., and *Bombus fervidus* (F.).

According to many apiculturists the colony needs influence the relative number of bees foraging for pollen and nectar. Heavy brood rearing, for example, may lead to increased pollen collection. However, the effect of such needs is spread over many kinds of plants. The percentage of bumble bees collecting alfalfa pollen varies greatly from day to day and from hour to hour. Whether this variation is associated with colony needs, availability of more attractive pollen, or atmospheric conditions is not known. Alkali bees (*Nomia melanderi* Ckll.) usually complete one ball of pollen each day, and most of the nectar is added to it when the final molding takes place in the late afternoon. However, whether they take nectar principally at this time or merely store it in the honey stomach during the day until the proper time for regurgitation has not been determined.

Competing sources of pollen and nectar have a strong influence on the number of bees that collect pollen and nectar from alfalfa. Most species of bumble bees, for example, prefer red clover to alfalfa, especially as a pollen source. When a red clover field comes into bloom, both the total number of bumble bees and the percentage of pollen collectors decline on nearby fields of alfalfa. Hobbs and Lilly (1954) in Alberta found that only in dry summers, when almost no bloom occurred on the prairies, could effective numbers of bumble bees and *Megachile* be expected on alfalfa-seed fields. The effect of such wild bloom on the percentage of alfalfa pollen-collecting bees was not stated.

Only when competing pollen sources are nearly eliminated over a large area is the number of honey bees collecting alfalfa pollen noticeably increased. Less drastic elimination is required in the case of most wild bees. This may be related to the relatively low flower constancy of most species of bees. With the alkali bee another reason may be that alfalfa is one of its favorite host plants.

The condition of the alfalfa plants affects both the total number of bees visiting the field and the relative numbers of pollen and nectar collectors. A moderately well-watered field with large, well-spaced plants seems to be the most attractive to nectar-

<sup>2</sup>Male honey bees don't visit flowers. Except for stingless bees (*Meliponinae*), males of all other bees do.

collecting honey bees. Pollen-collecting honey bees seem to prefer more limited moisture and are even more partial to adequate spacing. Little is known about the preferences of other kinds of bees. Alkali bees like dense, well-watered growth better than dry, sparse growth. I have often seen alkali bees concentrate on small patches of luxuriant growth in an otherwise poor stand. Furthermore, they like to fly inside the dense growth, visiting the innermost racemes as freely as the outer ones. It is not surprising that growers in "alkali bee areas" believe they get the highest yields with dense plantings, whereas progressive growers in "honey bee areas" are convinced that well-spaced plantings give them the best yields.

Some varieties and strains of alfalfa are more attractive than others to certain kinds of wild bees. Vansell and Todd (1946) noted that a strain designated as C-11 was especially attractive to several species of leaf-cutting bees. Subsequent studies (Pedersen & Bohart, 1953) showed that it was also highly attractive to pollen-collecting bumble bees. A strain from Argentina was found to be highly attractive to several species of leaf-cutting bees at Logan, Utah, but it was not unusually attractive to bumble bees or honey bees. The subject of varietal attractiveness to wild bees has received little attention, although it may have important possibilities. Many wild bees are very specific in their flower preferences and a small change in the floral characteristics of a variety of alfalfa might greatly alter its attractiveness to certain species. I have frequently observed that, whereas bumble bees are not abundant in the agricultural areas near Logan, small plantings of hairy vetch or red clover can attract them from large areas and concentrate effective populations. Small fields of a highly attractive variety of alfalfa might achieve the same result.

## POLLEN COLLECTORS

### POLLEN COLLECTORS ON TRIPPED FLOWERS

Bees visit both tripped and untripped flowers. Those visiting tripped flowers do so for the pollen they can scrape from the exposed stamens. Small halictids, andrenids, and colletids unable or scarcely able to trip flowers are the principal visitors of the flowers that are already tripped. Such bees are seeking pollen and make no effort to obtain the nectar still available in small quantities. Honey bees on rare occasions visit tripped flowers for pollen and take some nectar as well. In general, populations of small nontripping bees increase on a field when the rate of tripping increases. It is usually assumed that they play little part in pollination, since the receptive surface of the stigma is pressed against the standard petal after tripping. However, several authors such as Linsley (1946) have suggested that they may be important in cross-pollinating flowers not cross-pollinated at the time of tripping. If they actually play such a role, it is conceivable that tripping machines might succeed in areas where the bees are abundant enough to invade alfalfa fields in large numbers following use of the machine.

The genera most commonly visiting tripped flowers in Utah are *Hylaeus*, *Lasioglossum*, *Halictus*, and *Nomadopsis*. *Halictus arapahonum* Ckll. is the species most often seen, although in local areas of Millard County several species of *Lasioglossum* (*Chloralictus*) are sometimes more numerous. Larger halictids, such as *Halictus ligatus* Say, *H. rubicundus* (Christ), and *Lasioglossum sysimbrii* (Ckll.) utilize tripped flowers when they find them, but they also trip their own flowers when necessary (although with considerable difficulty). The same holds true for *Nomadopsis scutellaris* (Fowler), which visits alfalfa only when little else is in bloom. This bee is very abundant in Utah and Idaho, but has been observed as an important pollinator only in the Howell Valley of northern Utah. Even at this locality it deserts alfalfa as soon as Russian-thistle (*Salsola pestifer*) comes into bloom.

### POLLEN COLLECTORS ON UNTRIPPED FLOWERS

Bees visiting untripped flowers may or may not trip them. When seeking pollen primarily, they trip most of the flowers they visit and, except for the moderately small halictids and andrenids previously mentioned, have little difficulty in doing so. Most pollen collectors approach the flower facing the standard petal and insert their heads into the center of the throat or very slightly to one side. They usually use their



midlegs as braces against the wing petals while using head and mouth parts to apply a downward spreading pressure in the throat. This releases the sexual column from the enclosed keel petals and allows it to spring forward against the ventral side of the bee's head and glance off to the standard petal. Some of the smaller megachilids, such as *Megachile brevis* Say and *Osmia seclusa* Sandh., claw the keel apart with their forelegs and receive the blow from the stigma and stamens on their thoracic or even abdominal venter. Most pollen-collecting bees use their forelegs to scrape pollen from the stamens for a brief period during and immediately after the tripping process. In addition, they may get a general dusting from the small cloud of pollen released into the air by the force of the tripping. Thus, they can receive pollen by three routes. After visiting several flowers in rapid succession, the pollen gatherers take a brief "packing flight" to transfer the pollen from the receiving areas to the pollen-carrying apparatus.

Bees occasionally develop the habit of approaching the flowers over the standard petal, facing the keel. This is an individual rather than a specific characteristic. When a bee succeeds in tripping a flower in this manner, the blow from the sexual column lands on the front or top of its face.

Pollen-collecting bees probably take no nectar during most of their visits to alfalfa flowers. Although the tongue is in a position to take nectar while the flower is being tripped, it is rarely trapped against the standard petal by the sexual column. On the other hand, when nectar collectors trip flowers, they are commonly trapped in this manner. Perhaps the pollen collectors take a quick sip of nectar and retract the tongue in time to avoid being caught. Pollen-collecting bees in such genera as *Apis*, *Bombus*, and *Anthophora* often digress for various periods of time to take nectar by the normal methods described below for nectar collectors. *Megachile gemula* Cress. follows the same practice. However, most megachilids stay with pollen collecting although their honey stomachs often contain a little nectar, probably obtained during some of their pollen visits.

The tripping rate of pollen-collecting bees varies from less than 1 per minute for small bees such as *Halictus ligatus* Say to about 25 per minute for certain large bees such as *Xylocopa californica* Cress. and queens of *Bombus morrisoni* Cress. In general, the larger the bee the more rapidly it can trip flowers. However, megachilids seem to have a special knack for tripping alfalfa, and even small species such as *Osmia seclusa* Sandh. and *Megachile brevis* Say can trip about 14 flowers per minute as compared to 8 for honey bees, which are considerably larger. Large megachilids such as *Megachile dentitarsis* Sladen can trip about 20 flowers per minute.

## NECTAR COLLECTORS

Nectar-collecting bees sometimes insert the tongue directly into the throat of the flower in the same manner as pollen collectors. More commonly they insert it from the side between the standard petal and the inrolled upper margin of the wing petal, or behind the wing petal at the margin of the standard petal. Occasionally they use an intermediate approach at the inner edge of the inrolled margin of the wing petal.

### THE DIRECT APPROACH

Bees entering the throat of the flower between the wing petals nearly always trip it when they penetrate deeply enough to reach the nectar. Species of *Anthophora* with long, slender tongues and some of the long-tongued bumble bees are the only ones able to reach the nectaries through the throat without tripping a large percentage of the flowers. Some anthophorids can even take nectar without landing. Nectar collectors using the direct approach can usually be distinguished from pollen collectors by the absence of clawing movements and the relatively long time they leave the tongue extended. They may even fly from flower to flower without retracting it. Furthermore, they often fill up with nectar and return to the nest before the pollen-carrying areas are loaded. Sometimes nectar-collecting bees discard the pollen that strikes them, but more frequently they transfer it to their carrying areas. In the case of honey bees and bumble bees the pollen loads of nectar collectors are usually rather small and poorly formed.



Male bees and parasitic bees of certain genera sometimes use the direct approach. Males of *Nomia melanderi* orient their bodies in various ways but always try to enter the throat. More often than not they neither trip the flowers nor reach the nectar. Males of several genera of bees, such as *Anthophora*, *Diadasia*, *Agapostemon*, and *Halictus* are sometimes common in alfalfa fields but tend to be very "flighty" and rarely attempt to enter the flowers. When they do, they nearly always fail. However, males of the larger species sometimes learn to use the side approach successfully. Males of many species visit alfalfa even though females of the same species rarely or never do so—for example, *Agapostemon cockerelli* Crawford, *Diadasia enavata* (Cress.), and *Melissodes obliqua* (Say).

When the hairy-eyed cuckoo bees (*Coelioxys*) visit alfalfa, they brace their legs against the wing petals and force their heads against the base of the standard petal in much the same manner as their non-parasitic relatives, *Megachile*. However, they omit the clawing movements.

#### THE SIDE APPROACH

Bees using the side approach can reach the nectar quickly and easily and avoid contact with the sexual column. Furthermore, they don't have to spend time in pollen-packing flights. Experienced nectar-collecting honey bees are probably the most skillful users of the side approach. Depending upon various conditions, they trip from 0.2 to about 2.5 percent of the flowers visited. Some bumble bees are nearly as skillful. Nectar-collecting individuals of *Bombus huntii* Greene, for example, have been seen to visit as many as 30 blossoms per minute as against about 15 for honey bees. However, their rate of accidental tripping (caused by stray movements of the legs) is usually higher. Nectar-collecting bumble bees usually use the side approach. They insert the proboscis between the standard petal and the inrolled margin of the wing petals or even closer to the center, but never behind the wing petals.

*Anthophora urbana* Cress. is a very skillful side-worker. It visits flowers more rapidly than honey bees and, on the basis of limited observations, has at least as low a tripping rate. According to Franklin (1951), *Xylocopa virginica* Drury is just the opposite. Its body is so heavy and its tongue so broad that even when using the side approach it frequently causes tripping. Male bees in the families Apidae, Anthophoridae, and Megachilidae generally use the side approach. Male halictids and andrenids are more likely to use several approaches, most of them unsuccessfully.

### WILD BEES

#### ADVANTAGES AND DISADVANTAGES

Most alfalfa-visiting species of bees pollinate alfalfa much more efficiently than nectar-collecting honey bees and somewhat more efficiently than pollen-collecting honey bees. When sufficiently abundant they can pollinate the flowers so rapidly that only a light bloom is evident on the field at any one time. Under these conditions the seed crop is less susceptible to damage by sucking insects and certain diseases than it would be with slower pollination. The grower who has had experience with pollination contracts also appreciates the fact that his wild bees are "free" and don't bother him in the field.

The shortcomings of wild bees as pollinators are obvious for the most part. They are usually too scarce for adequate service, their populations are too unpredictable from year to year and week to week for reliable service, and such measures as have been devised for their maintenance and increase are often contrary to accepted agricultural practices.

#### CONSERVATION

The problem of obtaining and maintaining adequate numbers of wild bees on a seed field can be approached from the standpoints of populations in the area and on the field. High populations in the area are usually favored by (1) providing plenty of wild land for nesting (broken terrain with bare areas, banks, and patches of shrubby growth is usually the most attractive to a wide variety of species); (2) providing sufficient bloom in the area throughout the season to attract and provide food for the species in the area; (3) having as many species as possible; (4) maintaining existing

nesting areas and establishing new ones; and (5) avoiding the use of insecticides during bloom (when unavoidable, using materials least harmful to bees and when bees are not on the field). High populations on the seed field are favored by (1) timing the bloom for the period of greatest abundance of the most important species, (2) limiting the acreage in bloom at any one time, and (3) reducing competing sources of pollen and nectar during the blooming period of the seed crop.

Declining numbers of wild bees in new agricultural areas may be more a matter of diluting the existing population over increasing acreage than reducing the overall population. Farmers in frontier areas often expand legume acreages rapidly to improve the soil. Much of that acreage is devoted to seed because of the high yields that usually occur on the first few fields in a new area. When the acreage of bloom increases, the overall population of wild bees may also increase, although benefit from the increased forage is more often than not offset by destruction of nesting sites and careless use of insecticides. It is only under exceptional circumstances that wild bee populations keep pace with expanding acreage of bloom. When areas become more settled, limitation of nesting sites and destruction of adult bees by insecticides become more serious than dilution of existing populations. In this phase of more intensive land use, limitation of blossoming plants is likely to reduce wild bee populations still further.

#### INCREASE OF ALKALI BEES

Pioneer farming practices are sometimes responsible for increasing both the forage and nesting site conditions of certain species of bees. When this happens the species in question may increase as rapidly as the acreage of seed alfalfa. Eventually, however, specific conservation measures become necessary to maintain the advantage gained. The alkali bee in the Northwest provides an outstanding example. When farmers first appeared, the nesting areas for alkali bees were limited to a few areas of natural seepage. Furthermore, only a few of the native plants were useful to them, and they were limited to small areas in the larger valleys where natural moisture was available. Irrigation greatly increased the suitable areas for nesting, and the introduction and spread of cultivated crops and foreign weeds such as alfalfa, sweetclover, Russian thistle, and spearmint increased the available forage manyfold. Even such native host plants as bee flower (*Cleome serrulata*) were increased on wasteland and roadside areas.

In some areas, as pointed out by Bohart (1955), "improved" farming practices such as ditch lining and drainage of waterlogged areas have greatly reduced the populations built up by careless water use in the past. Furthermore, huge nesting grounds have been ploughed up to plant more alfalfa seed. In recent years alkali bees have been nearly wiped out in many areas by the use of such insecticides as parathion and dieldrin on blossoming alfalfa. The above measures have usually accomplished their immediate goal but in the end have depressed seed yields by "killing the goose that laid the golden egg." Fortunately, it is possible to maintain and even increase alkali bees without sacrificing good farming practices. Seepage areas can be prepared and maintained exclusively as nesting sites. Since alkali bees are highly gregarious (a million or more can nest in an acre of ground), the land devoted to their culture need not be large. Lieberman *et al.* (1953) have devised control programs for harmful insects that do not seriously reduce alkali bee populations. These programs have proved to be at least as successful in their primary objective as the programs that result in destruction of pollinators.

In the Riverton area of Wyoming, the Snake River Valley near Boise, Idaho, and the Yakima River Valley near Prosser, Washington, alfalfa-seed growers are already successfully preparing and maintaining nesting sites for alkali bees. Their ranks are increasing, and a few growers in other areas such as the Uintah Basin and Delta seed areas of Utah have signified their intention of preparing sites in 1957. This interest on the part of the more progressive growers is bringing to their neighbors greater awareness of the need for protecting bees.

At the present time alkali bees are largely responsible for high seed production wherever it occurs in the states of Washington, Oregon, Idaho, Wyoming, Montana, and northern Utah. Furthermore, there appears to be a great potentiality for increasing alkali bees and seed yields in many localities in these states.

## INCREASE OF OTHER WILD BEES

According to reports alfalfa-seed growers in northern Manitoba have had some success in maintaining populations of *Megachile* and *Bombus* on their fields. This they have done by limiting the cultivated areas to relatively narrow strips surrounded by native aspen and cottonwood timber growth. The timber cleared from the fields is piled around the field margins. Beetles boring in the wood provide nesting places for *Megachile*, and rodents nesting in the brush piles provide nesting sites for *Bombus*. Additional trees in the surrounding forest are girdled to furnish more nesting places for *Megachile*. I have not seen the area in question, but it seems probable that the favorable conditions created will be difficult to maintain for many years.

## INTRODUCTION OF POLLINATORS TO NEW AREAS

In many areas it should be practical to improve pollination by wild bees by the introduction of additional species. Apparently the only concerted efforts in this direction were made near the turn of the century when bumble bees were successfully introduced into New Zealand from England. Attempts during the same period to introduce bumble bees from England into Australia failed. Recently R. A. Cumber (1953) investigated the possibilities of introducing bumble bees from England to Australia, but was opposed on the grounds that parasites or diseases of honey bees might be introduced thereby. This fear, although understandable, was almost certainly groundless. Since only queens need be sent and these can be nematode-free individuals collected in the fall, there is little likelihood that parasites or diseases of either honey bees or bumble bees would be introduced. Mites might accompany the queens, but they are harmless scavengers in bumble bee nests and are in no way associated with acarine disease of honey bees.

Megachilids should be particularly well suited for introduction. The larvae develop well in confinement and are protected by cocoons in the overwintering stage. The cocoons could be inspected for evidences of parasitism and placed in split sections of hollow stems or drilled cylinders of wood (Levin and Haydak 1958) for shipment and release. Several species of *Megachile* have been accidentally introduced into eastern North America from Europe and one arrived in Hawaii from California. What man has done inadvertently, he should be able to do on a larger scale using purposeful methods. Other wood-inhabiting bees such as *Xylocopa* and *Ceratina* should be as easy to introduce as megachilids. Some of the *Xylocopa* are efficient alfalfa pollinators, but any species considered for introduction should be studied first to see if it damages structural timbers.

Many kinds of bees may prove to be difficult to transport and establish in new areas, but only actual trials will give us a clear picture of the problems concerned and lead us to the eventual solutions. There are many species to work with. Furthermore, many areas with similar climatic and soil conditions have entirely different bee faunas. Central Asia, being the homeland of alfalfa, is of particular interest as a source of alfalfa pollinators. Popov (1956) listed 22 species as being important alfalfa pollinators in central Asia. He gave special mention to *Melliturga clavicornis* Latr., a gregarious species nesting in open spaces of flat ground. Without doubt some of these species could be profitably introduced to various seed-growing regions. The alkali bee, an inhabitant of the intermountain areas of the West, would probably prosper in intermountain valleys of various parts of the world where alfalfa is grown.

## WILD BEES IN THE FUTURE

The future for wild bees in agricultural areas is not necessarily so grim as it has been pictured. Some of the species that suffer from intensive agriculture may fare reasonably well if the present trend toward more pastures and soil banks continues. Species that are highly gregarious and also useful as pollinators can be maintained in special preserves by enlightened farmers. Indiscriminant bloom-stage applications of insecticides harmful to bees is one of the worst problems to be faced. Research has shown that we can develop satisfactory programs for the control of harmful insects with a minimum of damage to bees. Unfortunately, the importance of measuring both aspects of the problem by the same economic yardstick has not been widely accepted by the various organizations and individuals concerned.

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# Factors Affecting Value of Bees (Hymenoptera: Apoidea) as Pollinators of Alfalfa and Red Clover<sup>1</sup>

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## ABSTRACT

*The value of a species of bee as a pollinator of alfalfa or red clover is sometimes dependent upon its physical limitations insofar as its ability to obtain nectar or pollen from various types of flowers is concerned. Physical limitations have been confused with the deterrent effect resulting from the structure of the flower; for example, the failure of the honey bee to gather pollen from alfalfa.*

*In northern latitudes, solitary bee pollinators should be winter-hardy, uni-voltine, and should emerge about 70 days before killing frosts occur. For colonial species, the peak of pollen-gathering activity for alfalfa and the peak of nectar- and pollen-gathering activity for red clover should coincide with the peak of the blooming period of the crop to be pollinated. Knowledge of these characteristics and of the nesting habits should enable one to understand whether the principal factors limiting population buildup are physical or biotic.*

*If competing growth cannot be reduced sufficiently to compel bees to obtain food from alfalfa when it is normally in bloom, blooming may be delayed by clipping to take advantage of the pollinating activities of late-flying bumble and leaf-cutter bees at a time when other food sources are depleted. However, if an early frost occurs much of this late-forming seed is destroyed before it has time to mature.*

*Much has yet to be done on the ecologies of the various species of native bee pollinators before methods of management are likely to increase their densities on the fields to be pollinated at a time when pollination will result in the production of mature seed.*

## INTRODUCTION

In Western Canada, legume seed growers rely to a great extent on native bees to pollinate red clover (Hobbs, 1957) and alfalfa (Hobbs and Lilly, 1954; Hobbs, 1956; Peck and Bolton, 1946; Salt, 1940; Sladen, 1918; Stephen, 1955); most of the seed may still be grown on fields that border virgin prairie or bush, which are the nesting habitats of species of bumble bees, *Bombus* Latr., and leaf-cutter bees, *Megachile* Latr. The growers must rely on leaf-cutter and bumble bees to pollinate alfalfa, as honey bees do not accomplish sufficient pollination to set a seed crop of commercial importance in Western Canada (Hobbs and Lilly, 1955; Hobbs, 1957; Pankiw, Bolton, McMahon, and Foster, 1956; Peck and Bolton, 1946; Pharis and Unrau, 1953; Salt, 1940; Sladen, 1918; Stephen, 1955). For pollination of red clover, they should rely to as great an extent as possible on bumble bees as certain species prefer red clover to alfalfa or native bloom for nectar and pollen, and the workers of one or other of these species forage throughout the blooming period of red clover; honey bees apparently gather only pollen from red clover, and their densities are always much lower on red clover than on nearby alfalfa (Hobbs, 1957). Alfalfa seed growers must rely almost solely on leaf-cutter bees for pollination when red clover is grown for seed nearby as none of the leaf-cutter bees are attracted to red clover, whereas almost all of the bumble bees are attracted to it during that period when pollination results in the production of mature seed (Hobbs, 1957). Alfalfa seed growers may rely on those species of leaf-cutter bees that reach their peaks of activity in July, only when competing bloom on or near the nesting habitat is at a minimum (Hobbs and Lilly, 1954).

The trend of the research on the pollination of alfalfa in the regions where honey bees have not been impelled to pollinate it, is now toward the management of native bee populations. Overwintered queens of bumble bees are induced to nest in artificial domiciles, which may be later moved to the crops to be pollinated (Fye and Medler, 1954; Montgomery, 1952), or queens are introduced into domiciles and are held

<sup>1</sup>Contribution No. 3604, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

captive until they begin brood-rearing activities (Hasselrot, 1952). Leaf-cutter bees are being provided with a continuing supply of natural nesting sites in the form of rotten logs by felling additional trees every six years.<sup>2</sup>

The following are discussions of the problems of selecting the proper species for management programs, and of increasing the densities of these species on the fields to be pollinated.

### PHYSICAL LIMITATIONS OF CERTAIN SPECIES OF BEES

Perhaps the prime example of what may happen when the physical limitations of a species are ignored is that of the importation of bumble bees to New Zealand to pollinate red clover. One of the species, *B. terrestris* L., was introduced though the importing agencies had been warned that it often obtained nectar from red clover by biting holes in the bases of corolla tubes and was, therefore, probably worse than useless as a pollinator of red clover (Montgomery, 1951). This trait is probably the result of having too short a tongue to reach the nectary of the red clover flower through the throat of the flower.

In southern Alberta, honey bees are apparently unable to gather any more than enough nectar from LaSalle red clover to satisfy their immediate nutritional requirements; they always gather nectar from alfalfa when red clover and alfalfa are grown in the same vicinity (Hobbs, 1957).

As honey bees gather nectar from alfalfa by inserting their tongues at the side between wing petals and standard petals, it was thought that they did not have tongues long enough to reach the nectaries through the throats of the flowers (Salt, 1940). It is now believed that honey bees do not seek the nectaries through the throats of the flowers because they apparently want to avoid being struck by the sexual column (Hobbs and Lilly, 1955; Reinhardt, 1952).

### FACTORS AFFECTING ABUNDANCE AND DISTRIBUTION

Some of the species of bees that occur in a region are not abundant and are unlikely to become abundant because the region lies within the area of marginal distribution for the species. Whether the region lies within the area of marginal distribution for a particular species may be determined sometimes by comparing the numbers of this and other species deposited in collections at various museums throughout the range of the species. Studies may then be limited to those species whose populations are affected chiefly by physical or biotic factors, factors over which the researcher may be able to exercise some control.

Other inherited characteristics that affect the abundance and the distribution of a species are voltinism, flight period, and nesting habits. At Seven Persons, Alberta, in 1954, many of the second brood of the partially bi-voltine species, *M. perihirta* Ckll., and of the late-flying, uni-voltine species, *M. wheeleri* Mitchell, were deprived of food for their own sustenance, and for provisioning nests by a frost that killed all flowering growth before they were able to realize their biotic potential. Numbers of some species of leaf-cutter bees are limited by a lack of nesting sites; *M. frigida frigida* Sm., *M. inermis* Prov., and *M. pugnata pugnata* Say that prefer to nest in rotten logs are scarce or absent on the prairie but are common in the treed river valleys or older irrigated areas where planted trees have matured and died (Hobbs and Lilly, 1954). Hence, on the prairie, these species must be provided with nesting sites, or studies should be limited to those with abundant, natural nesting habitats at their disposal. In treed regions, however, sandy areas covered with *Pinus* spp. provide nesting habitats for the important ground-nesting pollinator of alfalfa *M. latimanus* Say (Peck and Bolton, 1946).

Similarly, certain species of bumble bees are apparently restricted to specific habitats by physical factors. Whereas 12 species were recorded from the treed river valley near Lethbridge when Hobbs and Lilly (1955) were attempting to eradicate them from the environs of an experimental field, only five were recorded from the prairie at Hays, Alberta (Hobbs, 1957). The queens of *B. huntii* Greene were more

<sup>2</sup>Personal communication — Mr. T. V. Cole, Entomology Laboratory, Science Service, Canada Department of Agriculture, Brandon, Manitoba.

than twice as numerous as were all of the other species combined in the river valley, whereas workers of *B. huntii* were much less abundant than were those of *B. nevadensis* Cresson, *B. borealis* Kirby, or *B. fervidus* (Fabricius) at Hays. *B. borealis* was rare in the river valley and abundant at Hays; *B. nevadensis* was abundant in both habitats, and *B. fervidus*, though common in the river valley, was apparently more abundant on the prairie. *B. ternarius* Say and *B. occidentalis* Greene were common in the river valley but were not seen on the prairie at Hays. Reasons for these different affinities for more or less sharply defined ecological niches cannot be found in the scanty data on nesting habits. Two nests of *B. nevadensis* were found below ground, but five queens established nests in domiciles of the Fye and Medler (1954) type above ground. Six nesting sites of *B. fervidus* have been recorded, one on the surface, one below ground and five in Fye and Medler type domiciles above ground. Franklin (1913) found "many" nests of *B. fervidus*, all on the surface, and Plath (1922) found 13, one situated two feet above ground in a stone wall, four on the surface and nine below the surface. One queen of *B. borealis* reared a brood in a Fye and Medler type domicile above ground. All of those observed by the writer in their natural habitat were nesting in abandoned mice nests. Hence, it is unlikely that the habit of nesting on the surface or below ground limits a species to a particular habitat, and more will have to be learned about the ecologies of the various species before it will be known why certain ones are more abundant in one habitat than in another.

#### SYNCHRONIZATION OF BLOOMING WITH THE POLLINATING ACTIVITIES OF THE PRINCIPAL SPECIES

The time available for pollination and maturation of seed, and the flight periods of solitary species or the brood-rearing cycles of colonial species must be considered when evaluating a species as a pollinator. The time available for pollination and seed setting becomes less the farther north seed is grown. Most of the solitary bee pollinators that occur in Western Canada east of the Rocky Mountains have only one generation per year (Hobbs and Lilly, 1954); with favourable weather, almost all of the members of a population of a solitary species complete nest-building activities within 30 days (Bohart and Cross, 1955; Hobbs, 1956). Hence, the value of a species as a pollinator depends partly on whether the period of maximum bloom of the crop is synchronized with the flight period of the species. For late-flying species, it is relatively easy to retard blooming by clipping to coincide the period of maximum bloom with the flight period of the bee. However, as approximately 40 warm days are required for maturation of seed (Hobbs and Lilly, 1954), frost may destroy the maturing seed that resulted from the pollination of flowers by late-flying pollinators; a killing frost occurred at Hays, Alberta, on September 10, 1955, and alfalfa flowers pollinated after July 31, did not have time to set mature seed. Hence, where early frosts are a hazard, due consideration must be given to the probable interval between flight period and frost when adjustment of the blooming period is made. As the brood-rearing activities of species of bumble bees occur at different times (Hobbs, 1957; Plath, 1922), the species that produces the pollen-collecting worker force when pollination will result in the production of mature seed will be the most important. In southern Alberta, *B. nevadensis* stops producing workers by the time alfalfa and red clover begin to bloom profusely; the peak of pollen-gathering activity for *B. borealis* coincides with the peak of the blooming period of red clover and alfalfa, and that of *B. fervidus* occurs as the bloom is waning (Hobbs, 1957).

#### EFFECTS OF COMPETING GROWTH ON DENSITIES OF BEES ON LEGUME SEED FIELDS

An abundance of food is probably a main factor contributing to an increase in the abundance of a species; it may also be a main factor in the decrease in the densities of a species on a crop when the abundant supplies of food consist of two or more species of plants. The bloom of some species of plants are definitely preferred to others as sources of nectar or pollen by certain species of bees. The principal species of prairie bumble bees preferred red clover to alfalfa as a source of nectar and pollen

(Hobbs, 1957). Honey bees flew over alfalfa to gather pollen and nectar from sweet clover, *Melilotus* spp. (Hobbs and Lilly, 1955), and flew over red clover and native Compositae to gather nectar from alfalfa (Hobbs, 1957). One species may be preferred to another by a bee when the two species are approximately equidistant from the nesting site of the bee, but when the so-called preferred source is farther from the nesting site, many of the bees will utilize the nearer source until it is depleted. When late-June rains helped to produce abundant bloom on certain Compositae on the prairie in southern Alberta, *M. perihirta* apparently utilized these sources of food rather than fly from its prairie nesting sites to the alfalfa flowers on the irrigated fields bordering the prairie (Hobbs and Lilly, 1954). One female of *M. perihirta*, whose nesting activities were observed for three days in 1955, made alternate trips to nearby thistle and to alfalfa half a mile away, perhaps going to alfalfa because its nectar was more easily obtained than was that of thistle. In 1955, at Hays, Alberta, although little pollination took place on a rectangular, three-acre field surrounded by prairie, almost every flower was pollinated in 64-plant plots that were spaced at intervals of one-quarter mile across this same prairie; this indicated that the proximity of the food to the nesting habitat was an important factor.

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# The Inter-Relation of Insect Control, Soil Fertility and Pollination by Honeybees in Seed Production of Forage Legumes, as seen by Research in Minnesota

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## ABSTRACT<sup>1</sup>

*In a program of research on seed production of alfalfa, alsike clover, red clover and sweet clover, in progress at the University of Minnesota, pollination is the most important facet. Wild bees have been found to be either not available, or, if available, not present in sufficient numbers for practical purposes. Currently, research on pollination is concerned with honeybees.*

*Flower competition is probably the most important factor in determining whether honeybees visit a particular crop or not. Sweet clover flowers are the most attractive followed by alsike clover. Alfalfa flowers appear to be more attractive than red clover. Whether alfalfa flowers are tripped or not is apparently dependent on honeybee behaviour which is itself dependent on a number of factors.*

*For another phase of the research, the following hypothesis has been advanced and studied. The amount of seed produced by a crop is dependent not only on whether or not the honeybee visits a particular crop and pollinates it, but also on the ability of the crop to produce flowers and to develop seed in quantity if pollination is available.*

*Field experiments with all four seed crops have been conducted in which the effect of the following factors on seed production has been studied singly and in combination: control of injurious insects, pollination and nutritional status of the crop plant as a result of fertilizer application. In these experiments, seed production of alsike clover has been as high as 808 lb. per acre; the average for the state is 114 lb. per acre. Seed production of alfalfa has been as high as 760 lb. per acre; the average for the state is 49 lb. per acre. Seed production of red clover has been up to 700 lb. per acre; the average for the state is 59 lb. per acre. Seed production of sweet clover has been up to 2,100 lb. per acre; the average for the state is 180 lb. per acre.*

<sup>1</sup>To be published in full elsewhere.





# The Genus *Megachile* Latreille (Hymenoptera: Megachilidae) and Alfalfa Pollination

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## ABSTRACT

It is generally accepted that profitable alfalfa seed-yields result from cross-pollination effected by various species of bees. The honey bee, unfortunately, is ineffective as a pollinator of this crop whereas certain of the native bees are highly effective. Of these, certain species of *Megachile* are the most efficient. Workers in various parts of North America have stressed the need for modified cultural programmes, designed to utilize and conserve the existing populations of native bees. Such programmes will have to be based on an understanding of the biology of the important bees in the area concerned. Since little was known about the habits of the species of *Megachile*, studies were made of those species found in the alfalfa fields of southern Ontario. The information gathered is summarized and discussed briefly with reference to seed production. Emphasis is placed on the need for a uniform method of evaluating the species of pollinators. These evaluations would then be used to determine the number of pollinators necessary to produce profitable yields. Such evaluations would also point out where the emphasis should be placed in a conservation programme, since our attention should focus upon the most efficient species rather than upon those that most readily lend themselves to management.

Throughout most of the legume growing areas of the world the trend in seed production appears to have been from moderately high yields 30 to 40 years ago to low, unprofitable yields at the present time. This is especially true of alfalfa, since commercially profitable seed yields can be produced only from flowers that have been tripped and in which cross-pollination has been effected. At present, there are no artificial methods of producing seed-sets in the open fields, thus seed-growers must rely on the activities of insects which visit the alfalfa flowers for pollen. In Utah and California honey bees have been used successfully; elsewhere certain of the native bees appear to be the only effective pollinators. With few exceptions, however, the numbers of native bees are limited and quite insufficient to handle the acreage of alfalfa devoted to seed production.

In southern Ontario, about 30 species of bees have been recorded from alfalfa (Pengelly, 1953). Many of these are of limited value because they are inefficient in tripping or low in numbers. The more important species are those of the genus *Bombus* Latreille (bumble bees), 1 species of the genus *Andrena* Fabricius, and certain species of the genus *Megachile* (leaf-cutting bees). The latter are the most efficient pollinators, rarely do they visit an alfalfa blossom without tripping it.

The biology is known for about 5 per cent of the bees of North America (Bohart, 1952) and, as he clearly indicated, we do not know where even the more important species nest. During the past few years more emphasis has been placed on the need for conservation and utilization of existing native bee populations. The possibility of designing a programme, to encourage the important pollinating insects to increase their numbers, is foremost in the minds of many workers in this field today. Such a programme, of necessity, will be based on an understanding of the habits of the bees concerned. Of the alfalfa pollinators in Ontario considerable information is available on the biology of the bumble bees, but as very little was known of the habits of the highly efficient leaf-cutting bees, studies were carried out on the bionomics of those species most commonly found in the alfalfa fields in this area, viz. *M. brevis* Say, *M. texana* Cress., *M. latimanus* Say, *M. melanophaea melanophaea* Sm., and *M. frigida frigida* Sm.

The number of leaf-cutting bees in the alfalfa fields throughout most of southern Ontario was extremely variable. For the most part, there were so few that full-scale biological studies could not be undertaken. Part of the Bruce peninsula, situated

between Lake Huron and Georgian Bay, possessed a relative abundance of species as well as individuals, thus the major portion of these studies were conducted in that area.

Field observations indicate that *Megachile* spp. in Ontario emerge about the middle of June and continue their activities until early September. Here, there is but one generation per year, although in the more southerly areas there may be as many as four (Michener, 1953). The length of the emergence period is not known but there is some evidence that it may be as much as 3 weeks. Cells from the nests of six species of *Megachile* were collected and stored overwinter in a screened insectary, with protection from precipitation and direct sunlight only. On June 10 they were transferred to the laboratory and, under these conditions, the first specimens emerged on July 3 and the last ones on July 20. On the Bruce peninsula, adult bees were never abundant during late June or early July and July 7 was the earliest date on which nests of any species were found.

Soon after emerging, the female bee begins the task of finding a suitable nesting site which varies with the species of bee concerned. *M. latimanus*, *M. melanophaea*, and *M. texana* nested in tunnels in the soil or under flat rocks on the surface of the ground. *M. centuncularis* frequented the cracks and crevices of the walls and roofs of buildings. *M. frigida*, although primarily a wood-nesting form, also nested in the soil and in cavities in rocks on the Bruce peninsula. *M. brevis*, perhaps the most versatile in this respect, is known to have nested in tunnels in the soil, cavities under rocks on the surface of the ground, tunnels in wood, hollow stems, corrugated cardboard, and rolled-up leaves.

After locating a suitable nesting site the bee constructs a cell or series of cells from oblong and round pieces cut from the leaves and petals of various plants. In southern Ontario 47 species of plants have been recorded as sources of nest-building material. However, of the many kinds of plants present in any one nesting area, only a small percentage were utilized by the bees. There was some indication that the bees had a slight preference for the leaves of the young trees but they were observed to gather leaf-pieces from the tops of tall maple trees (*Acer nigrum*) and basswood trees (*Tilia americana*), especially in late summer. In the prairie regions of western North America, the scarcity of suitable leaf-material is likely to be an important factor in limiting nest construction, and the planting of suitable bushes near the nesting areas was suggested by Peck and Bolton (1946) for the seed-growing regions of northern Saskatchewan. The problem of an adequate supply of suitable nest-building materials is one of minor importance in southern Ontario.

Data on the various phases of nest building and provisioning were obtained from detailed records on the activities of individual bees during the process of cell construction. It was not possible to obtain accurate data on the time spent by the bee in locating a suitable nesting site and seldom was the observer on hand when the first leaf-piece of the nest arrived. The majority of nests were located during the early stages of cell construction, thus most of the records taken of cell-building activities were incomplete.

The number of leaf-pieces in a single cell varied considerably from species to species, from individual to individual of the same species, and between consecutive cells of the same nest. On the average *M. frigida* used fewer leaf-pieces in each cell than did the other species, while *M. brevis* used more. The maximum for *M. frigida* was 29, that for *M. brevis* was 103. The differences in the nests of the various species with respect to the quantities of materials used were not constant.

The time spent by a bee in gathering a load of pollen is influenced by several factors. Among these are: the type, abundance, and availability of pollen plants; the age of the bee; competition from other bees; and weather. In general it required less time to gather a load of pollen from St. John's-wort (*Hypericum perforatum*) or cinquefoil (*Potentilla recta*) than from alfalfa (Table I). Each of the species studied at this time, required about 1 hour to gather a load of pollen from alfalfa whereas most pollen-collecting trips to other plants were considerably less.

During the first three weeks of July, flowers such as St. John's-wort, cinquefoil, ox-eye daisy (*Chrysanthemum leucanthemum*) and staghorn sumac (*Rhus typhina*)

TABLE I — Summary of Nest Building Activities of Six Species of Megachile in Southern Ontario, 1953-1955. (all times are given in minutes).

Species	No. of leaf-pieces in base and cup of cell	Time recorded for collection of cell material	No. of loads of pollen	Range of collecting time per pollen load	Time recorded for pollen-gathering	Length of egg-laying period	No. of leaf-pieces in the cap	Time to close cell	Recorded time for cell construction	Source of pollen
<i>brevis</i>	a. 28	115	14	5 — 25	193	—	—	—	308	St. John's-wort & cinquefoil as above as above
	b. 57	546	17	10 — 72	557	10	8	40	1153	
	c. 37(20)*	101	16	10 — 37	427	16	5	35	589	
<i>texana</i>	a. 24(6)*	36	10	9 — 20	173	2	10	56	267	as above
	b. 15	165	10	14 — 87	315	13	11	82	575	as above
	c. 28	245	10	48 — 63	600†	11	13	87	943	Alfalfa
<i>centuncularis</i>	a. 26	122	9	17 — 20	196	13	5	16	347	Mallow
	b. —(33)*	183	12	10 — 38	123	9	3	7	232	Mallow
<i>frigida</i>	a. 12	135	9	52 — 79	562	12	3	24	833	St. John's-wort
	b. 17(13)*	255	8	61 — 140	732	17	4	21	1025	Alfalfa
	c. 12	200	7 or 8	40 — 178	997†	15	3	24	1236	Alfalfa
<i>melanophaea</i>	a. 26(24)*	129	9	14 — 39	194	?	12	?	323	St. John's-wort & cinquefoil as above as above
	b. 26(9)*	81	13	14 — 76	477	?	10	?	557	
	c. 13(8)*	87	9	27 — 77	593	3	18	56	739	
<i>latimanus</i>	a. 20(7)*	89	16	18 — 32	575	39	20	52	755	as above
	b. 15(13)*	175	10	16 — 41	378	?	5	34	787	as above
	c. 24	155	10	57 — 93	702	16	15	86	959	Alfalfa

\*Number of pieces recorded in column II.

†Records not complete.

provided the bulk of the pollen used in provisioning the cells constructed by the leaf-cutting bees. As these blossoms faded there was a marked shift of these bees to nearby alfalfa fields, which then provided the majority of the pollen for them until the end of the season.

The mortality data obtained from 214 cells are summarized in Table II. Of the 48 adult bees that emerged from these cells 32 were females, an average of 1 female bee

TABLE II—Summary of Emergence and Mortality of Individuals from the Cells of Nests Constructed by Seven Species of *Megachile*, 1952 and 1953.

Species	Emerged		Not Complete	Did not Develop		Otherwise Destroyed	Total
	<i>Megachile</i>	<i>Coelioxys</i>		<i>Megachile</i>	<i>Coelioxys</i>		
<i>M. brevis</i>	8	14	2	10	1	1	36
<i>M. texana</i>	3	9	6	9	9	3	39
<i>M. centuncularis</i>	2						2
<i>M. relativa</i>		1					1
<i>M. frigida</i>	28	11	8	29	3	3	82
<i>M. melanophaea</i>			5	1			6
<i>M. latimanus</i>	7	6	6	16	9	4	48
Total	48	41	27	65	22	11	214
Per cent of grand total	22.14	19.16	12.61	29.91	10.25	5.14	

for every 7 cells constructed. If a single female can build 30 cells in a season (Packard, 1867; Michener, 1953) it appears that the leaf-cutting bees possess a potential for increasing their numbers under normal conditions with each female in one generation giving rise to 4 in the following generation. Parasitic bees of the genus *Coelioxys* were found in 29 per cent of the cells studied. It is of interest to note that this is the same as that reported for nests of *M. brevis* in Kansas (Michener, 1953). In spite of the relatively high mortality caused by all factors, the bee population should be able to increase under optimum conditions where each female constructs the maximum number of cells during her lifetime.

Cell construction is influenced by several factors, some of which come within the control of man. Of these, the more important are; the abundance and availability of pollen producing plants, the availability of adequate nesting sites, and severe competition from other pollen-collecting bees during periods of pollen shortage. The availability of suitable nest-building material is vitally important in some areas but not in southern Ontario. Rain and heavily overcast skies will interrupt nest-building activities and such conditions, if prolonged, will result in fewer cells being constructed. Temperature, under normal conditions, appears to have little effect on the activities of the bees. During the summer of 1954, which was relatively cool, female bees were observed to leave their partly completed nests as early as 6:50 a.m. at temperatures as low as 63 degrees F. The day's activities ceased between 5:45 and 7 p.m. at temperatures ranging from 64-75 degrees. Neither the duration of pollen-collecting trips nor the time spent in gathering leaf-material appeared to be reduced as temperatures increased. Flower-visiting rates were within the same range when temperatures were below 70 degrees F. as they were at 90 degrees F. or over.

From information such as that obtained in this study, an evaluation can be made of each species of bee that visits alfalfa for pollen. The majority of the comparisons made by research workers have been based on flower-visiting rates and tripping efficiency. Although these are of value, they do overlook the great differences in the habits that exist among the various genera and species of bees. Workers of the bumble bees for example, are not concerned with nest-hunting nor cell construction as are the solitary species and thus can spend much longer periods in the field gathering pollen and nectar. As there is only one generation of leaf-cutting bees per year in this area, their numbers will decrease throughout the season. The numbers of bumble bees on



the other hand will increase greatly over the same period. The foraging trips of the leaf-cutting bees are primarily for pollen. Among the social bees, many individuals gather nectar only and those visiting alfalfa rarely effect tripping or cross-pollination.

Data on the biology of the leaf-cutting bees indicate that a practical programme can be designed to conserve and even increase their numbers. Areas selected for seed-growing would be those in which farming is not intensified, and where topography and land values limit the amount of land that can be brought under cultivation. In areas where land values are high, farmers cannot become involved in the growing of crops from which the returns are low or uncertain.

On the Bruce peninsula wild flowers were the major source of pollen until about the third week of July. Stands of alfalfa that are to be used for seed production should be clipped or cut before the middle of June. In approximately one month the second-stand alfalfa will have begun to bloom, just at the time when the native bloom has all but disappeared. The timing of the bloom-period to coincide with the activities of the bees will achieve two things. The bees will be assured of a continuous food supply enabling females to provision the maximum number of cells and, at the same time, prevent the migration of solitary species to other areas when food sources dwindle.

Since there is considerable variation in the habits and effectiveness of the insects that pollinate alfalfa, some method of assessing the contribution of each species would be of value. For example, *M. frigida* visited an average of 20 alfalfa florets per minute, tripping almost all of these. Each cell of the nest received an average of 9 loads of pollen which were collected in a period of about 9 hours. A single female might construct 30 cells during its lifetime but the one complete nest of *M. frigida* studied at this time contained only 26. By calculation a female bee would visit 280,800 florets during the season. Seed pods examined contained an average of 5 seeds which, on the basis of 80,000 seeds per pound, would equal 7.8 pounds of seed. This figure is a theoretical maximum. It assumes that the bee will confine its activities to alfalfa and that every blossom tripped will set seed. It also assumes that optimal conditions exist, allowing the bee to build and provision at least 26 cells with pollen collected from alfalfa flowers. However, if all species of pollinating insects are treated in the same manner, we will have a fairly accurate gauge of their contribution to pollination.

On the basis of figures quoted the yields of 600-1000 pounds of alfalfa seed per acre, reported for the old seed-growing areas of this province, could have been produced by as few as 75-125 bees per acre. If these figures are doubled or tripled to approximate field conditions, there would be a maximum of 400 bees per acre. Population densities such as this are known to exist in parts of Grey and Bruce counties at the present time and, in all probability, existed in many parts of Ontario a few decades ago. There is little reason to doubt that persons in Ontario who, either in the past or at the present time, obtained profitable alfalfa seed-yields, owe their success to the activities of certain of the native bees. Observations on honey bees as pollinators of alfalfa in southern Ontario are in agreement with the findings of Salt (1940), Peck and Bolton (1946), Hobbs and Lilly (1955), and Stephens (1955). In Alberta, Saskatchewan, Manitoba, and Ontario, honey bees make, at most, a very meagre contribution to seed production. It is improbable that seed growing will ever be re-established in the old seed-producing areas of Ontario. High yields are a product of the pioneer areas and these will be short-lived unless concerted efforts are made toward the conservation and management of native bees.

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# The Pollinations of Birdsfoot Trefoil (*Lotus corniculatus* L.) in New York State

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Birdsfoot trefoil (*Lotus corniculatus* L.) is playing an increasingly important role on New York State farms. It is a hardy, deep-rooted perennial — not unlike alfalfa, but unlike alfalfa it is recommended for the hilly dairy farms and heavier soils of the state. Seed production has been a problem in New York State and it was thought that pollination might be a factor.

This was a general study concerned with several phases of pollination, including competition among pollinating insects, effectiveness of pollinating insects, and the availability of pollinating insects.

## COMPETITION

It is known that honeybees can distinguish between different levels of sweetness and prefer plants with a sweeter nectar. The methods used were those of Park (1932) in which the honey stomach was removed intact from the bee and the contents placed in a refractometer. In this work a Bosch and Lomb hand refractometer was used. Between twenty and twenty-five bees were taken for use in each test and of this number an average of fifteen would be carrying nectar loads large enough to obtain a reading. Park's research had indicated that ten bees carrying a sufficiently large load to be read would be satisfactory.

Several honey plants which could offer competition in any pollination project may be found in the central New York State area and five clovers, a mint, vetch, wild carrot, milkweed and blackberry were studied to determine the relative value of each insofar as competition was concerned. This portion of the study was undertaken in 1951 and 1954. During June, and most of July, birdsfoot trefoil yielded nectar which contained slightly less total solids than did competing plants. During late July and August it yielded nectar which had a slightly higher total solids content than did competing plants. With only one exception was the difference at all critical, and this was in the case of vetch. In most tests vetch secreted nectar more concentrated than that of competing plants. However, this was offset by the fact that vetch was not present in sufficient quantity to offer severe competition.

The results of the competition study showed it would be nearly impossible to raise the number of pollinating bees in a field of birdsfoot trefoil above the number found in a competing field, but it was demonstrated that birdsfoot trefoil would attract a large number of bees.

The flowers of birdsfoot trefoil are rather large and it was demonstrated that the nectar was very susceptible to dilution by both rain and dew. In one instance, a rainfall of 15/100 of an inch caused the total solids content of the nectar to fall from 32.9% to 14.4% in a three hour period. During a typical summer day the concentration of total solids rose during the day, reaching a high at about 3:00 P.M. Figures in one instance, and which are typical, are as follows: 9:00 A.M. — 18.9%; 12:00 P.M. — 30.6%; 3:00 P.M. — 39.4%; and 6:00 P.M. — 35.4%. Whereas, the susceptibility of birdsfoot trefoil to such environmental conditions was high, other competing plants followed the same pattern throughout the day, although not to the extent which birdsfoot trefoil did.

## EFFECTIVENESS OF BEE VISITS

One bee visit of short duration (four to ten seconds) to flowers of all ages can, in some cases, bring about pollination to the extent that a maximum number of seeds are produced. However, this does not always occur and more visits appear to be necessary to insure a maximum seed set.

An increased number of bees decreased the flowering period. Flowers which received no bee visits would remain open for as long as ten days, while flowers which

received ten to twenty-five visits per day, as in the open field, would remain open only about four days and flowers which were in cages and received upwards of two hundred bee visits remained open about three days.

The effectiveness of individual bee visits was studied both in the greenhouse and under caged conditions in the field. Under greenhouse conditions few seed pods were formed, although this experience led to the refinement of field methods. In the field, individual flowers were tagged and the number and length of individual visits were recorded. This portion of the research was time consuming and although data was obtained on over four hundred and six flowers only one hundred and sixty-nine produced seed pods. These flowers varied from one to eleven days in age, and the length and number of individual visits were varied. Statistically, the number was insufficient, but still conclusions offered themselves.

The fact that flowers of all ages — that is, from one to eleven days old — could, with a single bee visit, produce a large number of seeds was proved. Thus, the conclusion offered by this phase of the research was that factors other than pollination were responsible for the low seed yields obtained in New York State.

Since one birdsfoot trefoil seed pod may contain a dozen or more seeds, a single bee visit to birdsfoot trefoil is far more valuable than a single bee visit to the majority of the other clovers where a single bee visit usually results in a single seed.

The question which followed was whether or not increased bee visits would increase seed yield. Unpublished data obtained by Dr. W. L. Coggshall of Cornell University had failed to show an increase in seed yield in cages where the number of bee visits had been increased about seven times over that in the open field.

One thousand six hundred thirty-three tagged flowers in cages with bees, where the average flower received from one hundred to two hundred individual bee visits, produced eight hundred fifty-six seed pods with an average of twelve and four-tenths seeds per pod. In the open field where flowers received twelve to twenty-five individual bee visits, one thousand five hundred seventy-one flowers produced nine hundred forty-nine pods with an average of thirteen and one-tenth seeds per pod. Thus, again in field trials it was demonstrated that increased bee visits did not increase seed yield.

### AVAILABILITY OF POLLINATING INSECTS

In central New York State the average bee population was about one bee per square yard. In the average field, flowers received twelve to twenty-five bee visits during the flowering period. Large reserves of nectar do not accumulate and honeybees visit flowers at the rate of about twelve per minute.

Square yard counts were used to assess bee populations. The counts were made by walking in a straight line through a field and at a given number of paces, estimating an area a yard square to the left and one to the right and observing it for five seconds. The method is rapid and it is felt to be more accurate than some method whereby a plot is actually delimited. In 1951 and 1952, 4,950 square yard counts were made. In these counts 5,256 honeybees were observed. Interesting, however, was the fact that only two hundred seventeen wild bees were seen. In the area studied honeybees represented ninety-five and nine-tenths per cent of the total population. Few of the wild bees observed appeared to be more effective pollinators than the honeybee and the figure given here is a higher value than those given by other researchers.

### CONCLUSIONS

Recommendations for the pollination of birdsfoot trefoil (*Lotus corniculatus* L.) were that attempts to increase bee populations in central New York State would be of little and probably of no value. Central New York State has been one of the major honey producing areas in the state and although honey flows have been poor during the last decade a large number of bees are kept there. Apiaries of twenty-five to fifty colonies are quite common and are generally distributed about two miles apart throughout the area.

Where any doubt exists, square yard counts may be used to assess the bee population. The average field of birdsfoot trefoil contains from one thousand to three thousand flowers per square yard. Honeybees normally visit about twelve flowers per minute. In an average field, honeybee populations of one, or slightly less than one, per square yard will allow flowers to be visited from twelve to twenty-five times each.

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# Honey Bees as an Aid in Orchard and Blueberry Pollination in Nova Scotia

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## ABSTRACT

Generally, unfavourable weather in the spring and the rather low insect activity hamper the setting of fruit in Nova Scotia. Native insect counts show wide fluctuations from year to year and from farm to farm.

The scarcity of native pollination can be overcome by employing honey bees. Special techniques have been worked out to overcome certain difficulties springing from the foraging habits of the honey bees.

(a) Plants bid for insect visits on three levels: between species, varieties, and areas. The field force is directed to the most attractive source.

(b) A bee colony in a new location may extend the foraging range from a few hundred feet on the first day up to a mile on the third. In scattered fields, rotating colonies every few days will overcome the spreading out of foragers. When the bloom conditions are constant, the foraging population is largely concentrated inside the four hundred yard range, and it tapers off to near zero within one and a half miles.

(c) The foraging area of a bee is somewhat less than the spread of a tree.

(d) Pollen for cross-pollination in orcharding may be provided by pollinizing varieties. Processed pollen is used when suitable varieties are not present or do not synchronize in bloom date. Processed pollen is given in pollen inserts placed in the hive entrances.

## INTRODUCTION

The Annapolis Valley of Nova Scotia is the oldest fruit growing area in Canada. Less than 50 years ago it was not only the main apple production area in Canada but also the chief overseas supplier to the English market. The loss of this market in combination with other factors has brought about the sharp decline of this industry in Nova Scotia. Recent trends in many producing areas have been to increase tree yield, but in Nova Scotia yields generally have declined. In good years, the Valley is still capable of producing about 20 per cent of the Canadian crop but more often than not the fruit set is light.

The low-bush blueberry, *Vaccinium angustifolium*, and related species, is an important commercial plant native to northeastern United States and Eastern Canada. Rocky barrens, abandoned farms, and other submarginal land are capable of producing huge quantities of these berries. In recent years the production in Nova Scotia has been between 3 and 5 million pounds of berries annually; in New Brunswick about the same; and in Maine about 18 million pounds. The industry as a whole is expanding, and the potential is tremendous, especially if Newfoundland and Quebec are included.

Cool wet weather during the bloom periods of apples and blueberries in Nova Scotia is only too common. Such unfavourable weather during these periods adversely affects the fruit set by reducing pollen viability, hindering the fertilization processes and suppressing insect activity.

## METHODS AND RESULTS

In orcharding the problem of cross-pollination is a matter of having a supply of suitable pollen and pollinators to transfer it. Suitable pollen is usually provided by setting out mixed varieties, interplanting pollinizing trees, grafting limbs into trees, etc. This pollen must be viable, compatible, and available at the time when the stigmas are receptive. When there is a scarcity or absence of suitable pollen from the above sources, processed pollen may be used instead.

The transfer of pollen to the stigmas, in the case of the apple and blueberry, seems to be almost entirely carried out by insects and hence the problem was to work out methods that would tend to increase the effectiveness of insect pollinators. These methods, which will be discussed briefly, are outlined in the N. S. Department of Agriculture and Marketing mimeographed paper #67, "The Place of Honey Bees in Orchard Pollination".

Insect counts, taken in a number of orchards throughout the Valley since 1951, revealed a rather low native insect population which fluctuated widely from year to year (Table I).

TABLE I — Insects Working Apple Bloom, Average per Tree in 15 Minutes.

Year	Honey Bees	Solitary Bees	Bumble Bees
1951 — 6 orchards	1.9	8.5	2.6
1952 — " "	0.5	4.9	2.3
1953 — " "	0.4	1.7	1.2
1954 — " "	25.4	2.7	3.4
1955 — " "	13.2	4.8	1.8
1956 — " "	10.8	6.0	1.8

Certain fringe areas where natural nesting sites for native pollinators are present, consistently showed higher counts than the Valley floor where good nesting places are scarce (Table II).

TABLE II — Insects on Apple Bloom, Average per Tree in 15 Minutes.

	Honey Bees	Solitary Bees	Bumble bees
1954 { Mountain slope	17.8	6.0	5.5
1954 { Valley floor	30.2	1.0	1.5
1955 { Mountain slope	7.2	4.8	2.1
1955 { Valley floor	18.0	3.3	1.8
1956 { Mountain slope	11.1	8.1	2.4
1956 { Valley floor	10.2	3.6	1.2

Observations in blueberry fields indicated the same wide fluctuation from year to year and from field to field. Such surveys established that low insect populations contributed largely to the problem.

The logical way of increasing the pollinating force was to employ honey bees. Initial trials using fairly large numbers of colonies of bees moved into orchards prior to the bloom were not encouraging. The bees appeared to work most of their potential flight range, which in the spring would be about 2000 acres.

Honey bees possess a remarkable ability to direct the foraging population to the most profitable crops. Once an abundant source of nectar or pollen is found, the area worked by the individual bee may be too restricted to effect, in the case of fruit trees, proper cross-pollination.

In the competition between plants for insect visitors, pears and at times apples have the disadvantage of secreting a lower quality nectar, than other species within the flight range. Bloom in one orchard block may be more attractive than the rest; certain varieties attract more visitors (e.g. Wagener is preferred over Gravenstein and MacIntosh). Soil texture, fertility level, slope, sunlight, shelter, etc., also exert their influence.

Before indicating possible methods of reducing the effect of the above-mentioned obstacles to effective pollination, consideration must be given to the dispersal rate of

field bees. Members of established colonies in blueberry trials could be found up to  $1\frac{1}{2}$  miles away. On a new site, however, the colony flight at first is confined to the vicinity of the hive and expands only gradually. Bonnier (1906) and Oettingen-Spielberg (1949) have shown that searchers become foragers and vice versa.

In a new location, most of the outgoing bees will act as searchers for a while and the displaced foraging population will pay rapt attention to dances of the returning searchers. Sardar Singh (1950) has demonstrated that 'fixed' bees, when confronted with a change of locality, will switch to new crops.

The expansion of the flight range on a new site in orchards is difficult to follow because bees from the experimental colony cannot always be identified. Smith (1951) described a method of studying the colony dispersion with the aid of fluorescent markers. Limited use of this technique has been made when testing the efficiency of pollen inserts under Nova Scotia conditions.

It was assumed that the dispersal rate of bees in the spring would be approximately the same regardless of the plant species. This phase was studied in the low-bush blueberries because large isolated fields with uniform stands were available. These studies were conducted in 1955 and 1956. Of these fields, two were about 800 yards in length and the third more than 900. Bee colonies were placed at one end of the field, and a series of strings were laid to mark the distances at 75, 150, 225, 300, 450, 600, and 750 yards.

During the first half-day, the bees in the new locality stayed within the 150 yard marker but before nightfall some bees could be found just outside the 300 yard mark. The bulk of the population, however, was still inside the 225 yard string. This corresponded with our observations under orchard conditions. Apart from the weather factor, the rate of dispersal appears to be governed by the amount of forage within the given area. In the case of sparse bloom in an orchard, bees (in the 1954 studies) abandoned the nearby source within a few hours to begin foraging the same crop in another orchard 400 yards away.

On the second day, in the blueberry field, scouting bees could be found well beyond the previous day's limit, and two bees were observed at the 600 yard line. The dense population near the hives had decreased by the second day which seems to indicate that the scout bees had expanded the foraging range and only the 'fixed' bees remained. This observation is strengthened by the fact that on subsequent days, the population in that area showed no apparent decrease.

In the 1955 studies by the third day, a few bees could be found beyond the 750 yard mark, with two being observed at 1500 yards. Consequently, in the 1956 studies, the colonies were replaced with new ones as soon as the first bees were observed approaching the 500 yard mark. In these studies three groups of three colonies were used. It took these groups 3, 4, and 4 days, respectively, before their field bees reached the marker.

Because of unsatisfactory experience with colonies moved into orchards at the commencement of the apple bloom and left for the duration of the bloom, and because of observations supported by the above findings, the following recommendations have been made:

- (1) delay moving in the colonies until conditions are right — i.e. enough bloom present, and weather favourable;

- (2) scatter the colonies throughout the orchard and select wind-protected and sunny sites;

- (3) replace the colonies with others as soon as it becomes evident that the bees are working areas, or bloom other than that intended. This rotation of colonies is preferably carried out every third or fourth day. Fruit growers several miles apart may pool their bee sources by exchanging the colonies.

- (4) use pollen inserts in cases when the compatible pollen for cross-pollination is lacking — (e.g. in solid blocks of one variety), in mixed varieties of mostly triploids;

where pollinizing varieties are not in bloom; when anthers are not dehiscing because of previous rain, etc. Processed pollen given to colonies in pollen inserts at the time of their initial flight in the new locality has, in our experience, greatly stimulated the bees to search for that particular source. Bees upon coming into contact with the pollen eagerly sample it, gather small amounts in their corbiculae, and re-enter the hive. Soon afterwards, much increased activity is evident both within and outside the hive.

Hagerup (1954) has pointed out that some close relatives to the low-bush blueberry, viz, *V. uliginosum*, *V. myrtillus*, bear fruit in Arctic regions where pollinating insects are few or absent. Further tests in Copenhagen with bagged plants, and with plants under glass in compartments where they could not be reached by the wind, have demonstrated that autogamy is a regular feature but only when the blossoms are shaken by the wind.

Blueberry plants, in the Blueberry Sub-station at Tower Hill, New Brunswick, which were exposed to wind but inaccessible to insects have failed to produce fruit. Artificial air blasts were also of no avail. Bell (1955) has demonstrated that, in our region at least, the low-bush blueberry blossoms must be insect pollinated to set fruit.

The plant yields both nectar and pollen. The nectar concentration, of course, varies from day to day but is about the same as that of apples and *Rhodora* which in some quarters are considered the chief competitors. In 1955 studies, concentrations varied from 37.5 percent to 58.8 percent solids with a mean of 48.6 percent and in 1956—from 36.2 percent to 59.1 percent with a mean of 47.8 percent. Notwithstanding the fact that the plant yields pollen which is readily gathered by the bumble bee, the pollen is largely inaccessible to the honey bee because the anthers are hidden in the narrow-mouthed bell-shaped blossom, and only the stigma reaches the level of the corolla mouth. Nevertheless, in the absence of other pollen sources, bees do gather some blueberry pollen which can be seen as tiny loads in their corbiculae. Evidently they remove it from the mouth parts and the clypeus which do come into contact with the anthers. Newly released bees working the bloom show clear evidence of pollen in their baskets but this disappears as soon as pollen from other sources is available. The plant thus has to be discounted as a pollen source for honey bees and hence one should not be unduly perturbed to find bees at considerable distance working good pollen sources. Bees were observed working wild strawberries, sorrel, and other less known minor pollen plants.

It is a peculiar working habit of the bumble bee that in gathering pollen from blueberries, the insect takes a firm hold on the flower and then shakes it by vibrating the folded wings for a fraction of a second. The blossom droops on account of the weight of the bumble queen, and the shaken pollen evidently runs down through the narrow cannula of the anthers into the lap of the insect. Only bumble bees which gather pollen or both pollen and nectar shake the blossoms but straight nectar gatherers do not.

Difficulties arise when it comes to establishing statistically the value of honey bees as blueberry pollinators. While experimental evidence is hard to get, our results seem to indicate they are of value. Honey bees work the bloom freely, even in the presence of competing plants such as apple trees in full bloom. Nectar secretion is not affected to any extent by cool weather and is quite copious. Colonies in blueberry fields, even in rocky barrens devoid of other honey plants, invariably build up as fast as in selected honey producing locations. Most colonies store some surplus honey from this source, and the strongest have yielded up to 40 lbs.

Some blueberry fields with excellent bloom in 1955 were not picked because it did not pay to harvest the very light crop. The failure was blamed on the lack of pollinating insects. The 1954 yield per harvested acreage in Nova Scotia was 909 lbs. per acre (Retson 1955). More recent figures are not yet available. By comparison, fields where honey bees were used yielded a ton of berries per acre, with the best fields yielding up to two tons.

The number of bee colonies used by growers in the blueberry pollination this year again showed an increase of more than 350%. This was the direct result of the growers' observations on yield results in previous years.



Recommendations for use of bees in blueberry fields vary according to whether there is or is not area competition. Large barrens, and isolated fields a mile or more away from other blueberry fields would fit the first category. In this case, colonies are either moved in at the time when the bloom opens or they are kept there for some time beforehand. Colonies should be kept in low-land localities where willows, maples, and dandelion abound previous to the blueberry bloom in order to stock up on pollen. Thus fewer bees would be directed to gathering pollen while the colonies are in the blueberry locations. This procedure could be improved still further by adding combs with pollen or by feeding a pollen supplement.

Since the native insects have preferred nesting places and their flight range is rather limited, bee colonies should be placed strategically. The same points as outlined in the orchard pollination should be observed in other respects.

The second alternative is used in fields where the adjacent territory offers additional bee pasture especially other blueberry fields thus distracting substantial numbers of field bees from the field to which they were assigned. In this case moving in colonies should be delayed until the first blossoms of the clusters are fully open. These colonies should be replaced with new ones every three or four days.

This latter method may seem rather laborious. However, this is the method that has been in use in our highest yielding fields for three years and results amply repay the extra work.

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# Pollination Studies in Apple Orchards of Western Norway

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## ABSTRACT

Investigations were carried out in 1950-53 in order to evaluate pollinating insects in relation to variable fruit set in Gravenstein, the principal apple variety in Norway. Since this variety is biannual, two trees, about 20 km apart (approx. 13 miles) were observed in 1950 and 1952, whereas two different trees in the same areas were observed in 1951 and 1953. Certain branches of each tree were counted for visiting pollinators during the entire blooming period. When weather conditions permitted, counts were made every other day from 1 to 11 hours per day.

Diagrams are presented to show the number of bumble bees, honey bees, and solitary bees in relation to temperature, sun, and precipitation records. A table showing the number of clusters under observation, bee units, per cent fruit set, etc., for each tree each year is discussed.

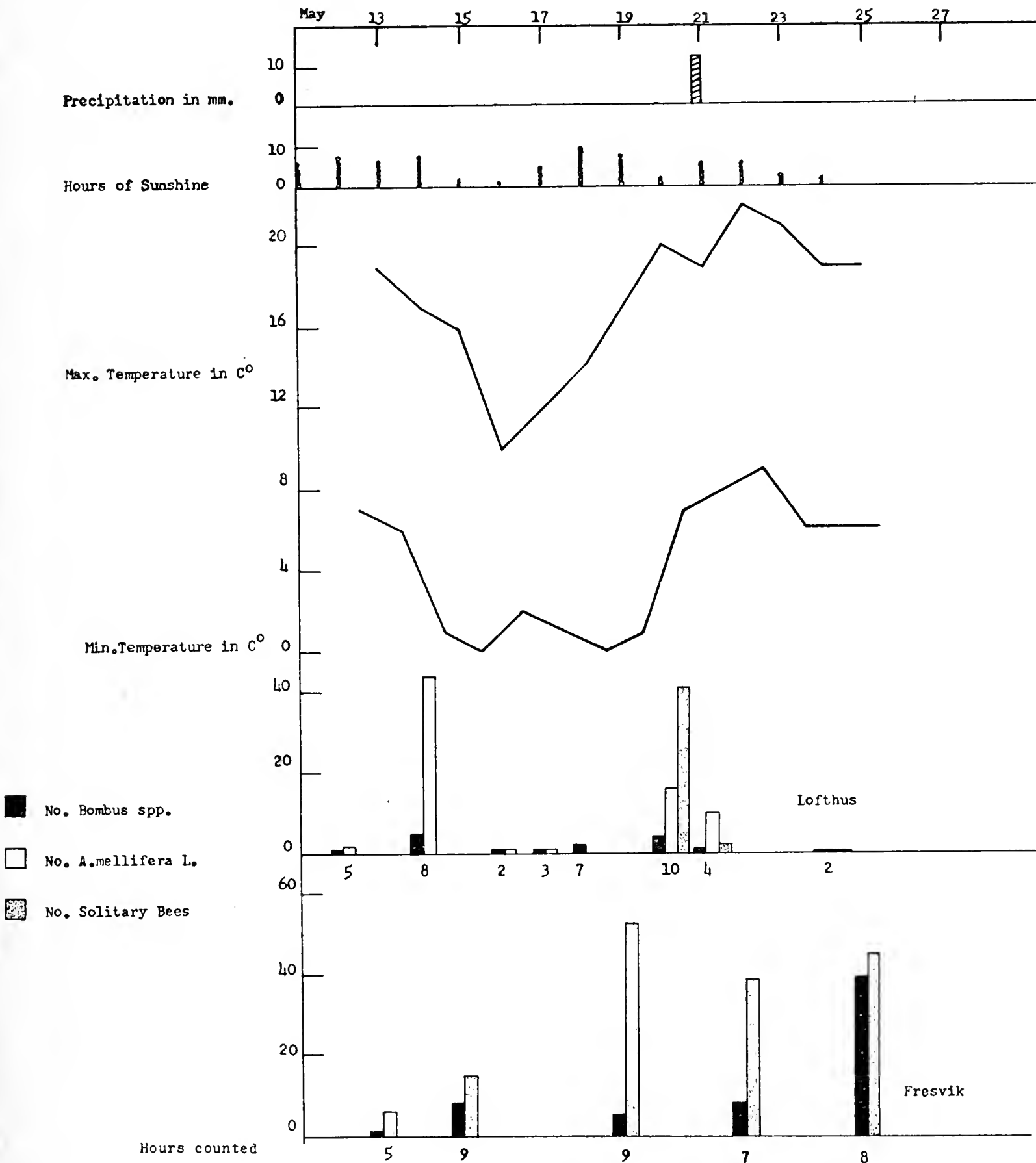


Fig. 1. Bee activity in relation to weather conditions 1950.

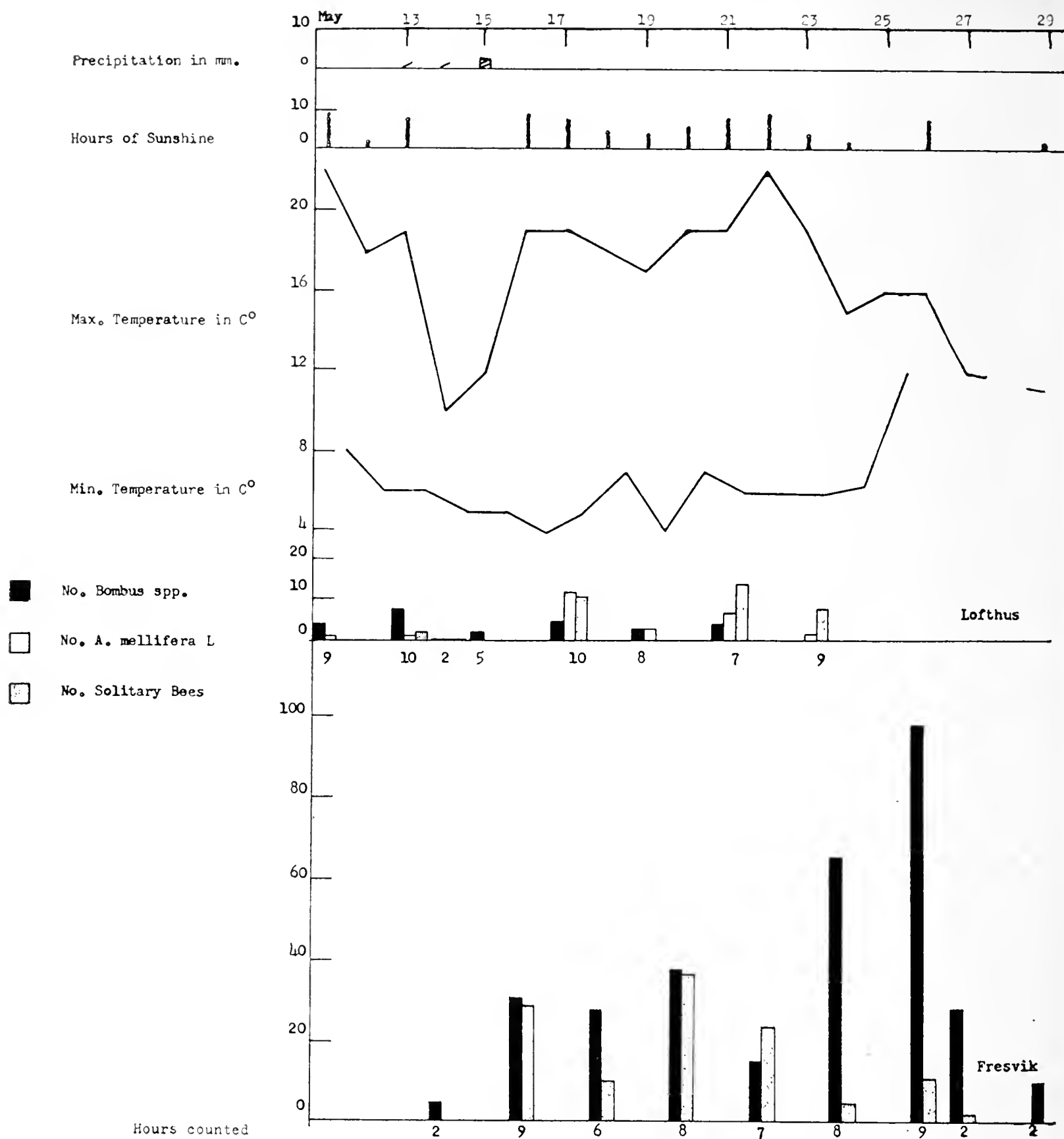


Fig. 2. Bee activity in relation to weather conditions 1952.

The research was carried out in Hordaland County, Ullensvang district in 1950-53. It was conducted to evaluate pollinators in relation to variable fruit set in Gravenstein, a principal apple variety in Norway. The paper will not be concerned about the fact that this variety is visited by fewer pollinating insects than other varieties which blossom contemporaneously. However, beside being triploid, the structure of the flower, particularly the filaments, form a barrier around the nectary and may reduce the attractiveness to many bees.

Since Gravenstein is biannual, two trees, about 20 km apart (approx. 13 miles) were observed in 1950 and 1952, whereas two different trees in the same areas, viz. at Lofthus and at Fresvik, were observed in 1951 and 1953. On certain branches of each tree visiting pollinators were counted every other day during the entire blooming period; that is, when counts were made in Lofthus, no counts in Fresvik and vice versa. One hour counts were made from 1 to 11 hours a day depending on the weather conditions. On only a few days was there no insect activity at all.

Beside Apidae, other Hymenoptera as well as Diptera, Lepidoptera were included in the counts. As these are not important pollinators, only the bees are considered in the diagrams, (Figs. 1-4), which show the number of pollinators in relation to the prevailing weather conditions. The counts, each year, are correlated to the same number

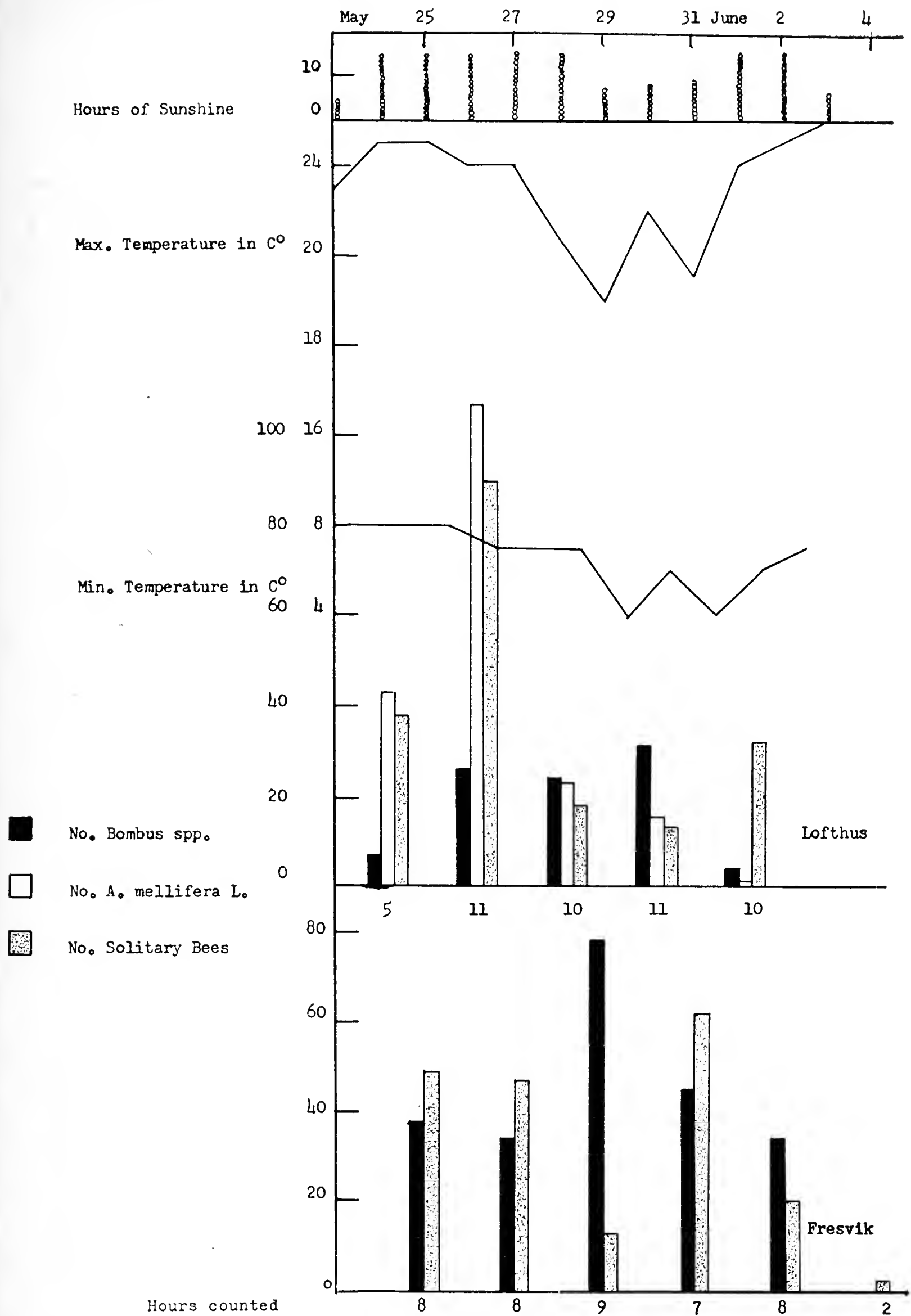


Fig. 3. Bee activity in relation to weather conditions 1951.

of clusters for both localities. In addition to the low temperatures in 1950 a light but steadily northern wind occurred almost every day. In comparing the counts in Lofthus 1950-52, the low visitation rate in 1952 is remarkable in that it does not coincide with the general activity in the vicinity. Figs. 3 and 4 reveal the great influence of weather on the pollinator activity. The high precipitation in 1953 reduced the hours of insect



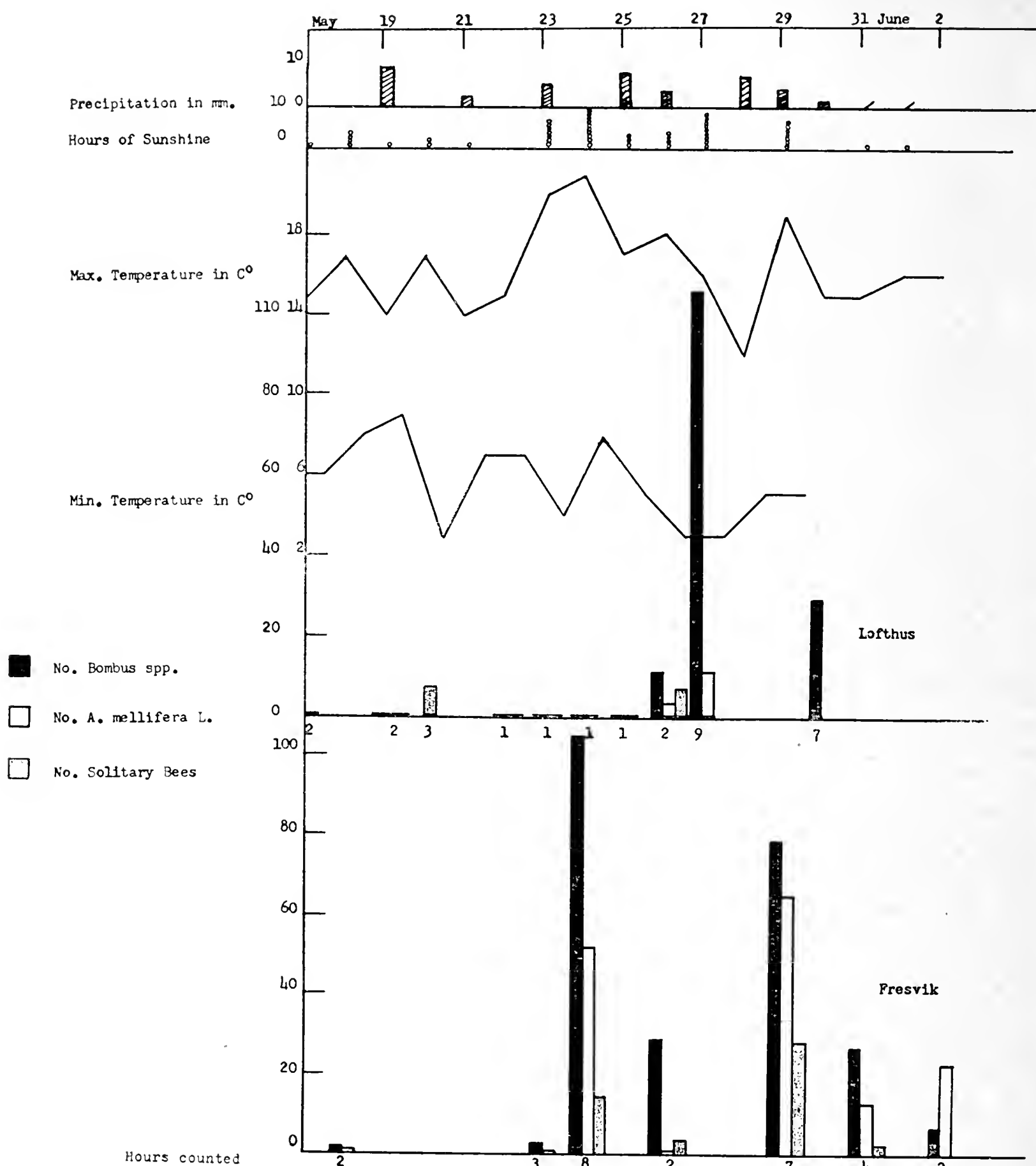


Fig. 4. Bee activity in relation to weather conditions 1953.

activity to the intervals of fair weather. However, the *Bombus* spp. particularly worked those hours with great intensity.

The counts, % fruit set and average no. of seed per fruit are shown together with the estimated "Bee Units" in the table. The Bee Units are based upon a rating of pollinating efficiency. As Gravenstein generally has flowers with the stigmatic surface of the pistils at a relatively great distance from the stamens, many bees collect nectar and even pollen without contacting the stigmatic surface. The respective pollinating efficiency of the bees is estimated as follows: bumble bees visit twice as many flowers per minute on the average than do honeybees. Each visit is "efficient", that the stigmatic surface is contacted. Whereas only about 50% of honeybees thus make contact. Each bumble bee is therefore given 4 times as many Bee Units as a honey bee. Solitary bees behave in the same manner as honey bees but visit on the average only half as many flowers per minute. *Bombus* spp. should probably be given a higher value as they often work during weather conditions where other bees do not fly. In Table I the estimated Bee Unit per cluster of flowers is calculated by at first

TABLE I — Fruit and Seeds per Fruit in Relation to Bee Units.

Locality	Year	No. of cluster	Hours of Observ.	No. of Bees Observed			Est. No. Bee Units per cluster	% Fruit Set	Av. No. Seeds per fruit
				<i>Bombus</i> spp.	<i>A. mellif.</i>	Sol. Bees			
Lofthus	1950	190	41	14	60	35	1.4	1.5	2.6
	1952	386	60	26	23	38	— .8	1.6	3.—
Fresvik	1950	237	38	60	0*	158	2.7	4.—	1.7
	1952	376	52	313	0*	116	7.—	4.3	3.4
Lofthus	1951	192	47	77	159	162	5.7	12.4	2.8
	1953	78	24	43	4	4	4.6	3.3	— .8
Fresvik	1951	235	42	229	0*	194	8.6	2.—	4.4
	1953	285	28	253	156	49	8.4	1.5	3.1

\*No colonies in district

*Bombus* spp. = 4 Bee units  
*A. mellif.* = 1 Bee unit  
Sol. bees = 1/2 Bee unit

assigning the respective species their Bee Unit value. Then it is assumed that each tree has been visited by twice as many bees as were counted, since while observations were being made at one location, bees also worked the other location.

The data show no relation between Bee Units and percent fruit set. The most striking feature is that each tree set about the same percent fruit in both years regardless of the number of Bee Units (1950-52) and the great difference in weather conditions (Fresvik 1951-53). The abnormally great percent fruit set in Lofthus (1951) may be due to the heavy fertilizer application that year. It is also strange to note that the tree in Lofthus (1950-52) while having a minimum of Bee Units had almost the same low fruit set as did the tree at Fresvik (1951-53) which had the maximum number of Bee Units. Both trees were between good pollinating varieties.

The number of seeds per fruit seems to be related to the number of Bee Units if the distance to pollinizer trees and the weather conditions are considered.

Even if problems concerning the fruit set need further investigations, the research indicates that, in general, the number of pollinators is not the limiting factor for the variable fruit set of Gravenstein in this district.

The counts include mainly the following bees:

- B. lucorum* (L.)\*

*B. agrorum* (Fabr.)\*

*B. hypnorum* (L.)\*

*B. pratorum* (L.)\*

*B. hortorum* (L.)\*

*B. mastrucatus* Gerst.

*B. soroeensis* (Fabr.)

*Andrena haemorrhoa* (Fabr.)\*

*Andrena jacobii* v. *scotica* Perk.

*Andrena cineraria* (L.)

*Halictus calceatus* (Scop.)\*

*Halictus albipes* (Fabr.)\*

*Halictus rubicundus* (Christ.)

*Psithyrus* spp

\*common



# Recent Studies on the Role of Honeybees in the Cross-Pollination of Small Seeded Legume Crops

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## ABSTRACT

*This paper is intended to deal primarily with the use of honey bees in the production of seed crops of alfalfa, trefoil, and clovers (ladino, red, alsike and strawberry) in California.*

*There is general agreement that adverse weather, harmful insects, and a deficiency in pollinating insects are factors most likely to limit legume seed set. Good crops result only when these three are absent and when the crop plants and soil moisture are managed correctly.*

*California legume-seed-producing areas are in general deficient in wild bees or other native pollinators. Honey bees are used. They are effective pollinators and can be increased or moved to meet demands. The number used per unit area is dependent upon the crop to be pollinated and on local conditions.*

*Methods of using honey bees in these crops have been developed. The placement within the field, time of introduction, and number of colonies to be used are important factors in production.*

*Bee management and breeding for pollination is being investigated to exploit the possibilities of producing a specific type of bee. These lines should excel in brood rearing, in pollen collection and have an affinity for pollen or nectar of legume crops.*

*Inadequate seed supplies of improved, adapted legume varieties have for years reduced the potential production of America's croplands. There are many different environments, each of which requires varieties having specific characteristics. These wide differences among the various adapted areas are conducive to the specialization of legume seed production in the western states.*

*Low yields of poor quality seed occur frequently in the humid eastern states, the large seed-consuming region. Here, weather, forage planting, and other conditions do not favor the regular year-after-year production and harvesting of improved forage-crop seeds. Seed production in regions of high forage production is usually an incidental farm enterprise.*

*Specialization in the production of legume seed with improved methods, and the opening of new areas in the western states where improved seed can be grown under state certification programs, is developing into an industry that may soon supply seed of known genetic purity and of high quality at prices competing with those paid for common seed.*

*The development of this industry was made possible through (1) release of new and improved varieties; (2) the discovery that first generation seed grown outside of the area of adaptation retained its hardiness, pest resistance, and productivity when grown back in its area of adaptation; (3) certification that safeguards genetic purity; and (4) farmers and beekeepers in California forming a team initiating the idea of producing alfalfa seed as a specialty product.*

*The success of their venture is evident in the production figures for the period of 1948 through 1955 (Table I).*

*The value of the 1955 alfalfa seed crop was more than 20 million dollars.*

*The varieties grown under certification and the estimated yield in pounds were: Ranger, 48 million; Buffalo, 5 million; Vernal, 4,500,000; Atlantic, 4 million; Caliverde, 2,500,000; Narragansett, 1 million; and Williamsburg, California-Common-49, African, Lahonton, and DuPuit, 1 million.*

*There were in addition 19 million pounds of common or non-certified seed produced, mainly California Common, African, and Indian. The acreage of certified*

TABLE I — A Summary of Alfalfa Seed Production in California 1948-1956, Including the Estimated Number of Hives of Bees Used in Alfalfa Pollination Service.\*

Year	Alfalfa certified	Seed in lbs. total common and certified	Yield in lbs./A.	Honeybees in State		
				Total no. hives	No. hives used in pollination service	Value of honey and pollination services
1948	446,000	4,500,000	215	442,000	52,325	3,150,000
1949	1,118,000	13,000,000	220	338,000	147,725	2,563,725
1950	4,502,000	31,000,000	270	451,000	287,115	3,271,230
1951	12,400,000	25,000,000	325	487,000	192,318	3,969,954
1952	30,944,000	39,000,000	475	521,000	205,266	7,059,798
1953	33,902,000	45,045,000	455	537,000	247,500	3,880,500
1954	39,951,000	58,320,000	440	537,000	308,685	4,538,055
1955	66,350,000	85,450,000	480	537,000	450,000	5,693,000
1956	?	?	?	548,000	400,538	5,544,614

\*Estimated yields were taken from the California Crop & Livestock reporting service.

alfalfa for seed production in California in 1956 is 120,628 acres or 14,515 acres below that of 1955.

The production of red clover, Ladino clover, Alsike Clover, and trefoil varieties has not yet reached the volume of production attained by alfalfa. The problems of production, however, particularly with reference to cross-pollination, are similar: all of these legumes require a medium to transfer pollen from flowers of one plant to those of another plant. For this service California seed growers must rely heavily on the domestic honeybee.

From 1942 to 1947 there were 457,000 hives of bees in California; about 75,000 of these were used in legume pollination services. By 1956 the number had risen to 548,000 hives, and more than 400,000 hives were used in legume pollination services.

The average return for honey and wax in 1942-47 was \$6.71 per hive. The average return for honey, wax, and pollination services in 1948-56 was \$8.79 per hive. The yield of surplus honey in 1942-47 was 45 pounds per hive. In 1948-56 it was 58 pounds per hive.

The improvement and growth of the apiary industry in California is evident and directly related to the substantial increase in legume seed production. The use of labor-saving devices, improved extracting plants, better bee yards, the standardization of hives as to brood, and the conditioning of hives to guarantee the seed grower a maximum bee population for pollination services have greatly improved the bee industry. Thus the seed grower has a guaranteed supply of pollinating insects and the beekeeper has a guaranteed income.

In specialized seed production, high seed yields that are dependable are most essential. The seed producers must manipulate their stands to take full advantage of favorable seed-setting periods to produce maximum yields. The seasonal variations and weather conditions are factors that effect seed production as well as honey, but over which the seed grower and beekeeper have no control. Therefore, production records over a period of years are needed to synchronize production with favorable weather history and to use long-range weather forecasting as a possible aid to further increases in seed and honey production.

The increase in per-acre yield and improvement in quality of alfalfa seed to date have been brought about through (1) better conditioning of stands for seed production; (2) better cultural practices; (3) better pest control of insects and weeds; (4) soil moisture control or improved irrigation; (5) controlled pollination; (6) spray-curing; (7) bulk handling of seed; and (8) improved harvesting and processing techniques.

Improvements in the beekeeping industry in California are a result of better management, improved handling techniques, and the greatly increased use of bees in legume pollination.



Domestic honeybees are essential in commercial legume seed production throughout the state. Their use as pollinators in the production of these crops in California is almost as common as the use of fertilizer to boost the yield of other field crops. Their continued use to accomplish the job of cross-pollination is certain.

The population and general distribution of wild and domestic bees in the seed producing areas of the state are not important factors in determining the number of bees needed for maximum seed production. Therefore, for all practical purposes, bees are imported and colonies distributed within seed fields. The arrangements of colonies, number of hives, time of placement in relation to the blooming period of the crop, condition of hives in relation to worker population and amount of brood, timing and formulation of insecticides to control harmful insects, and amount of competing pollen and nectar-bearing plants available are all factors that affect cross-pollination and seed production.

Honeybee colonies should be arranged in fields for accessibility, ease of service, and coverage. A convenient arrangement is to group hives 50 to 200 feet apart in lines or roads across the field, 400 to 1,000 feet apart.

From studies of hive groupings spaced at varying distance, it was found that 200 feet across the prevailing wind direction and 400 feet with it was favorable for field locations. Thus the bee hives would be 200 feet apart in one direction and 400 feet apart in the other. Roads and colony sites for this type of arrangement reduce potential production by about 2.2 per cent. It is believed, however, that the reduction in yield is of little consequence compared to the value of having the colonies well distributed over the field.

Time of placement is important. The first flowers that appear on young alfalfa are usually of little value in terms of possible seed set. For this reason it is considered good management to hold the first introduction of bees until the plants are in one-half to three-quarter bloom. The field should at least be well past the straggling bloom stage. In the early bloom stage one hive of bees per acre is sufficient. But in two to three weeks, bloom will usually have increased to the point where a second hive may be valuable, and in three to four weeks a third.

In tests conducted to determine the effect of rotating bees from field to field at intervals of 10, 20, and 30 days, rotation proved favorable to seed setting. Hives moved at any of the intervals improved tripping in the new field. The population of bees per square yard was also greatly increased. Moreover, in fields where all the bee colonies were removed for periods of five to seven days for application of insecticides, seed setting was favorable over fields where no rotation occurred. It is suggested that rotation of bees is a valuable practice in improving tripping because it increases the working population of bees in the seed fields.

The number of hives that may be profitably used to do a job of pollination depends on many factors. The following are important: (1) climatic conditions, length of season, temperature, wind velocity, rain, etc.; (2) bee activity, whether pollen and nectar collecting or nectar collecting only; (3) the prevalence of other pollen-bearing plants; (4) strength of hives or force of working bees; (5) proximity of bees to the seed fields; (6) the period of time that hives have been on location; (7) pest control operations in the locality or field; and (8) the condition of plants. Plants that are in the process of drying out or in stress for moisture may not be as receptive to seed setting as those that have sufficient moisture to maintain steady, slow growth. On the other hand, plants that are flush with growth also fail to respond to pollination to the best advantage.

The number of bees required to do a satisfactory job of tripping is quite variable. In tests conducted last season, however, it was evident that the tripping rate was closely related under all conditions to the population of bees per unit area.

For the nectar-collecting bees a satisfactory tripping rate was evident when a population of two to seven bees per square yard was active in the field.<sup>1</sup>

<sup>1</sup>Bee populations were based on counts of bees visiting one square yard blooming alfalfa. All bees visiting 42 such areas during one minute between the hours of 1 and 3 p.m. on three days each week for 20 weeks were counted. Tripping counts were also made on these plots over the entire period.

Tripping was very low when the temperature dropped to below 65° F.; the bee population dropped to about one per square yard. The rate of tripping was low during period when the wind velocity was above 10 miles per hour. Tripping was low for two to four days following an application of DDT or Toxaphene. Tripping was greatly improved when new colonies of bees were brought into an area.

The domestic honeybee is the important source of insect pollination in the production of legume seed crops in California. Seed growers and beekeepers are interested in ways and means of increasing their efficiency, feeling that much can be done to improve their performance. Much has been done through timely introduction, proper distribution, conditioning of hives, proper use of insecticides to control harmful insects, the control of weedy plants to reduce competition, and the conditioning of seed crops for maximum response to bee visitations. Other leads on crop response and bee management are being investigated. Plant breeders are interested in self- and easy-tripping lines. High nectar secreting and abundant rich pollen-bearing lines are also of interest to the plant breeder. In bee management breeders are interested in exploiting the possibilities of producing a specific type of bee, a line of bees which excels in brood rearing or pollen collecting, or with other factors or characteristics peculiar to it.

These investigations are being conducted cooperatively by agronomists, entomologists, beekeepers, and other specialists using the domestic honeybees and wild bees with but one goal: the improvement of legume seed production.

# Orchard and Legume Pollination in Ontario

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## ABSTRACT<sup>1</sup>

Recent studies tend to emphasize the fact that the pollination of fruit and seed crops is a specialized business, and that simply placing colonies of honeybees beside an orchard or legume field is not enough to obtain the maximum pollination benefit from them. Since each crop has its own specific requirements, efficient pollination may call for the services of an operator whom we might term a "Pollinator specialist". The number of colonies he used for pollination, and their placement would require a knowledge of many factors such as:

1. Seasonal effects — such as temperature, wind and colony strength on bee flight.
2. The crop to be pollinated, and the behaviour of the bees on that particular crop.
3. Competing sources of bloom, and their relative attractiveness to bees in relation to the crop to be pollinated.
4. Provision for proper cross-pollination in orchards, including the use of pollen inserts where necessary.<sup>1</sup>
5. Proper timing in moving bees for pollination in relation to the stage of bloom of the crop.
6. Avoidance of losses through spray poisoning.

Such an operator would need to stay with his bees on location to make sure that they did a proper job. Since a day or less of good flight may be sufficient to effectively pollinate an orchard, once this is accomplished the bees could be moved to another location. Thus the same lot of bees, properly managed, could earn the operator a number of rentals during one blooming season.

As pollinators, honeybees occupy an important place in our agricultural economy. It is up to the beekeeper to realize this, and try to contribute the services of his bees in the most effective manner.

<sup>1</sup>For further information on the fourth factor mentioned above, see: *Canadian Journal of Plant Science* 38: 39-44. January, 1958.



# Principles and Methods for the Utilization of Bumblebees in Cross-Pollination of Crops

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## ABSTRACT

The applied entomologist has long recognized that bumblebees are effective pollinators of many important agricultural crops, particularly legumes. It is postulated that bumblebee colonies can be successfully managed, and that bumblebee populations can be increased to the numbers necessary for the controlled cross-pollination of a wide variety of crops.

The successful management of bumblebee colonies will require a fuller knowledge of the biology and ecology of the various species. Previous investigators have made important contributions to our knowledge. However, much still remains to be learned before the bumblebee can be utilized for pollination under man's control. Some principles advanced at this time as a possible guide to the future research are as follows: (1) Queen control — The bumblebee queen should be kept under control during fall mating, winter hibernation, colony initiation, and during the pre-worker emergence period. (2) Colony control — Colonies should be domiciled, not only as a means of controlling environmental factors, but as a practical measure enabling movement of colonies from place to place and concentration of bumblebees on crops during pollinating periods. (3) Species diversity — Various species should be included in a management program in order to obtain the full advantage of different colonial cycles, and different flower preferences. (4) Selection and propagation of genetic stocks — The species of bumblebees should be studied with the objective of selecting races which have superior domestication and pollination habits.

The increase of bumblebee populations will be attained by a manipulation and control of the biotic and environmental factors, which in nature are responsible for the year to year fluctuations in the colony size. Important biotic factors are: (1) queen vigor, (2) ratio of brood to workers, and (3) inherent behavior pattern of the species. Important environmental factors are: (1) shelter, (2) food supply, and (3) freedom from enemies.

The principles and methods of bumblebee management are discussed in relation to the contributions in the literature and results of research in progress at the University of Wisconsin.

Students of bumblebees very early dismissed the idea that bumblebees could be used to produce honey for human consumption; but students and laymen both have continuously recognized that bumblebees are extremely valuable as pollinators of numerous flowers, including those of many important agricultural crops. In Eastern North America, one of the major unsolved problems of alfalfa and red clover seed production is inadequate pollination. Under certain exceptional conditions, a measure of pollination has been attributed to honeybees, but it seems unlikely to the writer that consistent success will be attained with honeybees in alfalfa and red clover seed production in Wisconsin. Consequently, the legume pollination research in Wisconsin is directed to studies of native bees. Of the many wild bees which visit legumes, the bumblebees are especially promising for study because of their colonial habit and their efficiency in collecting pollen. However, it is recognized that adequate pollination by bumblebees also cannot be attained satisfactorily unless the bumblebees are controlled and managed by methods which are consistent with the large acreages, the different flowering periods, and the varying degrees of floral attractiveness which are involved in modern crop production. Therefore, for the controlled cross-pollination of such crops, it must be postulated for the future that bumblebee colonies can be successfully

<sup>1</sup>Associate Professor in Agronomy and Entomology. Supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation.



managed and that bumblebee populations can be increased to the numbers necessary for practical results.

Eminent students of the biology of bumblebees have each directed some attention to the problems involved in the domestication of bumblebees. Sladen's (1912) book "The Humble-bee" is subtitled "Its Life History and How to Domesticate It". Sladen devoted a chapter to the manipulation of field domiciles in England, and reported on his experiments to obtain colonies by confining queens in artificial nests. As a requisite for complete domestication, he was convinced that both pairing and hibernation could be accomplished under human control. Frison (1923) included a wealth of valuable data relative to the domestication of Mid-Western bumblebees in his monumental Ph. D. thesis, most of which was published in a series of papers in several journals. Frison used field domiciles in his early research, but later because of his success in getting queens to rear their brood in confinement, he discontinued the use of domiciles as a means of securing colonies for his biological studies.

The present and future generations of bumblebee students will gratefully build upon the foundation provided by Sladen, Frison, Plath and other investigators of previous generations. Much still remains to be learned about bumblebees and their management. As a possible guide to the future research, and with a hope that more research will be stimulated, I am presenting this discussion on the principles and methods which might be used in domesticating bumblebees and utilizing them for pollination; but I hope especially to show where our present knowledge is inadequate for full accomplishment of such an objective.

### QUEEN CONTROL

Many years ago Sladen wrote: "By far the most interesting individual in the humble-bee family is the queen." To supplement Sladen at this time, it is important to emphasize that a full understanding of the biology of the queen is essential to bumblebee husbandry. It is postulated that successful management of colonies depends upon complete control of the queen during (a) fall mating (b) winter hibernation (c) colony initiation and (d) the pre-worker emergence period.

#### (a) FALL MATING

There seems to be no difficulty in mating bumblebees in cages. Sladen (1912, p. 140) placed queens and males of *B. lapidarius* (L.) in boxes with wirecloth covers and reported much copulation. Frison (1927b) confined males and queens in quart glass fruit jars, the tops of which were tightly covered over with several layers of cheese cloth and the bottoms of which were lined with corrugated paper. Frison recorded successful matings of *B. americanorum* (Fab.), *B. bimaculatus* Cress. and *B. vagans* F. Smith. Medler and Hunt (Wis. Agr. Exp. Sta. Rept. 1950, unpublished) placed a domiciled colony of *B. americanorum* in a  $2\frac{1}{2}' \times 2\frac{1}{2}' \times 3'$  screen cage, and at one time observed 4 queens *in coitu*.

One method to be followed in obtaining mated queens involves the rearing of queens and males in domiciles, isolation of the sexes for a period of time prior to placing them together in a suitable mating cage, and supplying the bees with food while in confinement. Another possible method utilizing artificial insemination will be discussed in a later section.

#### (b) WINTER HIBERNATION

Sladen (1912, p. 140) tried to winter bumblebees without success. Frison (1927b) reported repeated failures in his experiments, but did obtain hibernation of 4 of 11 queens of *B. americanorum*, those queens being ones which were placed in paper mailing tubes within fruit jars and cans on October 1st, and then buried in a mound of earth. The 4 queens were allowed their freedom in April. Frison believed that large numbers of well-fed, fertilized queens placed in hibernating quarters at the proper time of year could be successfully hibernated by his methods. Medler and Hunt (Wis. Agr. Exp. Sta. Ann. Rept. 1950, unpublished) attempted hibernation of queens which were placed in mailing tubes and buried in the ground or stored in a  $40-42^{\circ}$  F. refrigerator. None of the tests were successful. Medler and Fye (Wis. Agr. Exp. Sta. Ann. Rept. 1953, unpublished) attempted hibernation of *B. borealis* Kby., *B. fervidus* (Fab.), and *B.*

*vagans* queens in screen cages containing about 12" of soil and surface litter on top of the soil, but without success. Norgaard Holm (personal communication) hibernated bumblebees at Logan, Utah in wooden blocks buried in the ground. The queens were placed in holes drilled in the blocks, the holes were covered with screen, and the block covered with beeswax.

It is obvious that the unsolved problems of hibernation must be studied in both physiological and ecological aspects, the latter especially in regard to temperature and humidity requirements; and the former with regard to hormone control, metabolism, respiration and differences between mated and virgin queens. For example, it is not known if queens must undergo an obligatory period of cold accumulation or what determines the early to late appearance of different species. A degree of flexibility in habits is probable, since Cumber (1954) reported on queen bees flying on warm, sunny days in mid-winter in New Zealand, and on other modifications of life cycles of species introduced from England.

The writer believes that critical laboratory studies must provide the information so badly needed before a practical method of controlled hibernation can be developed.

### (c) COLONY INITIATION

This has received considerable attention because it has provided a means of securing the nests of bumblebees for study and experimentation rather than depending upon the chance location of nests in nature. The first observation on the construction of the first egg cell was made with a confined queen by Hoffer (1882-83). Sladen (1912), Lindhard (1912), Frison (1926), Plath (1934), Hasselrot (1952), Wilcke (1953) and Fye and Medler (1954b) have obtained colonies by various techniques. However, a critical review of this literature shows the empirical basis of the experiments. My own experiments have convinced me that much fundamental research remains to be done before a consistent and practical method is available.

At least four methods of colony initiation have been used:

(1) Transfer nests which have been started in nature. It is generally reported that the best transfers are made after development of the first brood to late larval or the pupal stages in order to discourage desertion by the queen.

(2) Provide artificial domiciles which are searched out and accepted by queens in nature. A refinement of this method is to release queens in a greenhouse with flowers and nesting material available.

(3) Place captured queens in an empty nest in nature.

(4) Confine the queen in a laboratory nest.

Although bumblebee colonies have been obtained with each method, the results are erratic and undependable. The queen is actually under control with the last method only, and I therefore believe that the future research should be concentrated on the initiation of nests in the laboratory. In the past this has been done by various manipulations, as follows:

(1) A single queen confined.

(2) Two queens confined together.

(3) A queen confined with brood taken from another nest.

(4) A queen confined with 2 or 3 workers collected in the field.

Sladen (1912) had no success with single queens of *B. terrestris* (L.) confined in a box. By placing two queens together the production of egg cells was accomplished, but one of the queens always killed her companion, and the developing brood was later abandoned. His best success was with pairs of queens, to which were added captured workers after the eggs were laid. Sladen produced a populous colony of *B. lapidarius* by uniting 2 small clusters of cocoons and seven young workers with a searching queen. He attributed the large worker force produced to the fact that the queen was able to proceed at once, while she still possessed the energy of youth, to

continuous egg laying in a prosperous colony without the delays and, more especially, the exhausting labor, of gathering food.

Lindhard (1912) utilized a two compartment nest box, one serving as a feeding chamber, the other as a brood chamber. After the queens started nest building, they were allowed to gather pollen from bouquets placed in the room where the boxes were kept, or they were permitted to forage in the open.

Plath (1923, 1934) reported on the rearing of 23 colonies belonging to 10 New England species over a 6-year period. Only colonies of *B. vagans* and *B. impatiens* Cress. were produced from queens confined individually in nest boxes, and as soon as the queens oviposited they were given their liberty. It was Plath's supposition that it would be impossible to rear colonies of pocket-makers (e.g., *B. fervidus* and *B. americanorum*) by confining queens, unless the queens were permitted to collect pollen from flowers, since the pocket-makers feed their larvae through pockets which are constructed at the side of each group of larvae, and the foraging bee deposits the pollen directly into these pockets.

Frison (1927a) gave a detailed account of his method of rearing colonies in artificial nests. He duplicated the requirements of the bumblebee with respect to nest material, honey pot, bits of wax, and a small compact mass of pollen, so that only the construction of the egg cells remained for the queen bent on laying eggs. Frison claimed as good results when one queen was used as when there were two. However, a critical analysis of Frison's 1917, 1919 and 1920 data shows that his chief success with one queen was with *B. perplexus* Cress. and *B. impatiens*, neither of which were compared with 2 queens; and that his most successful 2-queen experiments with *B. bimaculatus* were not adequately compared with a one-queen test of that species. Frison calculated his success as 29% in 1917, 77% in 1919 and 77% in 1920. I re-examined his data on the basis of the species concerned, and found his success more nearly 50% for any one species. Also, his success in the 3-year period, excluding starts only, was 41% for 2-queen tests and 59% for one-queen tests.

Using Lindhard's two compartment system, Hasselrot (1952) reported successful colony initiation of *B. terrestris*, *B. hypnorum* (L.) and *B. lapidarius*, by the confinement of one queen until she had laid first eggs, and then allowing her freedom in the open. Also, he mentioned starting two colonies of *B. terrestris* following refrigeration of the queens from April 27, 1951 to August 9, at which time they were placed in boxes. The started nests were observed on August 18, and on Nov. 5 males appeared.

The experiments discussed above have contributed to our knowledge of some of the requirements of artificial nests. But our knowledge is incomplete regarding the basic requirements of the queen for colony initiation, and more especially, the exact nature of the stimuli which induce egg laying and brood rearing. Critical research is needed on the physiology of the queen in relation to her nesting behavior. At my laboratory at the University of Wisconsin, I have been unsuccessful with empirical rearing tests with confined queens. My present research is largely concerned with pollen requirements of confined queens, the development of ovaries, and response to various temperature conditions; but this research has not progressed sufficiently for publication of any conclusions.

It is probable that controlled colony initiation will be a practical success only when single queens of each species can be confined under laboratory conditions which are conducive to consistent rearing of brood, and when a minimum of human manipulation is required.

#### (d) PRE-WORKER EMERGENCE PERIOD

It should be no problem to maintain the brood until the appearance of first workers under the suitable nesting conditions and proper handling which induced colony initiation. In fact, the development of the colony should be hastened by the relief of the queen from foraging activities, by the optimum conditions of temperature and humidity, and protection of the brood from natural enemies. It is a well-known observation of bumblebee students that only a few of the numerous queens that appear in the spring succeed in establishing colonies in nature. Nesting failure does not seem to be so much associated with unfavorable weather as with the attack of natural enemies. It is believed

that unfavorable environmental conditions could be eliminated in the laboratory. However, there may be other problems which will need attention. I have observed in domiciles the start of colonies which are inexplicably abandoned; perhaps by death of the queen while foraging, but also by an abnormal condition of the developing brood. Critical experiments will be necessary to determine whether the method of allowing a queen her freedom to forage naturally once eggs are laid, and risk her loss, has advantages over the continued confinement of the queen until workers appear. Following the appearance of the first workers, the colony probably should be moved into the field for a period of natural foraging and the population build-up.

### COLONY CONTROL

Bumblebee colonies should be domiciled not only as a method of obtaining control of environmental factors but also as a practical technique in the management of the bumblebees for pollination, which requires movement of the colonies from place to place and their concentration on crops during pollination periods.

It is well known that, in general, bumblebees utilize rodent nests in two situations: 1) on the surface of the ground, or just below the surface and 2) well under the surface of the ground. It might be hypothesized that a subterranean nest gives the best protection from the environment, including temperature and humidity control, and in this connection it is interesting to note that among the subterranean nesters both *B. terrestris* in Europe and *B. impatiens* in North America are very populous bees.

The first experiments on artificial domiciles were conducted by Sladen (1912). He provided a protected excavation in the ground in which suitable nesting material was placed in order to attract the searching queens. The majority of colonies obtained by Sladen were of *B. lapidarius*, but also obtained were *B. terrestris*, *B. ruderatus* (Fab.), *B. hortorum* (L.), *B. latreillellus* (Kby.), and *B. sylvarum* (L.).

Frison (1926) used buried domiciles similar in principles to those used by Sladen, but modified them with respect to the type of container and entrance tunnel. He reported successful colonizing of his buried domiciles by *B. americanorum*, *B. auricomus* Robt., *B. bimaculatus*, *B. separatus* Cress., and *B. impatiens*.

Major problems associated with the underground domiciles are excessive moisture, invasion by rodents and ants, and the labor involved in their installation and maintenance.

Wilcke (1953) and Fye and Medler (1954b) found that wooden box domiciles supplied with nesting materials were readily utilized by bumblebees. The boxes were placed on the surface of the ground or above the ground. A study of temperature conditions in several types of surface domiciles by Fye and Medler (1954c) showed that a wooden box aided the bumblebees in obtaining as satisfactory temperature control as the more elaborate types. The boxes are attractive to ants, especially in areas of sandy soil, but the ants can be controlled by an application of dieldrin on the underside of the box. Mice are excluded to large extent by a metal plate with an  $\frac{1}{2}$ " entrance hole. Excessive moisture conditions are avoided by the use of wood.

In Wisconsin, colonies of *B. fervidus*, *B. borealis*, *B. griseocollis* (DeG.), *B. americanorum*, *B. bimaculatus*, *B. vagans*, *B. rufocinctus* Cress. and *B. auricomus* have been obtained in box domiciles. Properly constructed boxes seem to provide the conditions suitable to bumblebees, namely, darkness, dryness, and protection; and of the species listed above, all but *B. americanorum* and *B. bimaculatus* have produced colonies in boxes which exceed in numbers those found in nature previously recorded in the literature.

Wooden box domiciles should be utilized in the management of bumblebees for pollination because the boxes can be easily handled and moved from place to place. It might be necessary to develop other types of domiciles for subterranean species, but it is possible that a wooden box can be placed in a subterranean location, and then moved from one underground location to another. Hasselrot (1952) reported on the successful initiation of *B. terrestris* in the laboratory and subsequent location of the box on a pole in the field. It is therefore a possibility that a subterranean nesting species, once colonized in a box, may not require an underground location for its development.



## SPECIES DIVERSIFICATION

A careful flower census in relation to the visits of various species of bumblebees should be made in each major crop area. Proper attention can then be given to the increase of the species which are most suited to the pollination of crops concerned. For example, it may not be practical to domesticate *B. terrestris* for red clover pollination, since this species is a short tongued bee and has a strong tendency to bite through the tube of the corolla near the base, thus having little value for pollination (Skovgaard, 1936).

The flower preferences of bumblebees have been reported by many observers and it is well established that numerous plants in a large number of plant families are attractive, including important crop plants in the Rosaceae, Leguminosae, and Compositae.

Bumblebees as a group are very reliable pollinators of legumes, but differences exist among the species as to their relative importance. In Wisconsin, *fervidus*, *americanorum*, *borealis*, *vagans*, *griseocollis*, and *auricomus* show a strong preference for red clover (Fye and Medler 1954a). These species can be managed in box domiciles. *B. terricola* Kby. readily goes to alfalfa and is a very important pollinator of alfalfa in Wisconsin. Attempts to attract this species to subterranean domiciles and surface box domiciles have been unsuccessful. There seems little advantage in propagation of *B. rufocinctus* and *B. ternarius* Say for legumes in Wisconsin since they seem to prefer composites. Several species will no doubt be used in a complete program, so that full advantage can be taken of the different colonial cycles.

A classic example of the value of bumblebees as pollinators is provided in the history of red clover seed production in New Zealand. No native bumblebees were available, and the importation and establishment of species from England was followed by a remarkable increase in the seed yields. Dumbleton (1948) and Montgomery (1951) reported on the three established species: *B. ruderatus*, *B. terrestris* and *B. latreillellus*. Sladen, (1912, p. 157) mentioned that the attempted introduction of *B. lapidarius* was a failure.

There seems to be no insurmountable difficulty to the importation of bumblebees from one region into another and the utilization of the introduced species for pollination. Queen control during mating and hibernation would eliminate the danger of nematodes and diseases being introduced into areas where they are not presently established.

The earliest attempts of shipping entire nests of bumblebees into New Zealand were failures. Apparently, the successful introduction was achieved with queens collected in the autumn in England and shipped under condition intended to hold them in hibernation until arrival. Frison (1928, p. 195) reported that a start of a colony was obtained with 2 queens of *B. bimaculatus* shipped in the spring from New York to Illinois. Cumber (1953) discussed methods which might be used in obtaining queens for shipment.

In the spring of 1955, I successfully air mailed 4 queens each of *B. auricomus*, *B. griseocollis*, *B. fervidus* and *B. impatiens* to Dr. R. E. Fye in New Mexico. The queens were placed in wooden block cages similar to honeybee queen cages, and provided with queen candy made from confectioners sugar and honey. I am confident that live queens can be air mailed to any place by this technique.

## SELECTION AND PROPAGATION OF GENETIC STOCKS

One of the basic principles of scientific agriculture is the application of genetic methods to the development of superior germ plasm in domesticated plants and animals. This principle should be applied to bumblebees with an objective of breeding them for better domestication and pollination habits. Some species are more vicious than others. *B. americanorum* and *B. fervidus* in North America are especially aggressive against man, and propagation of a gentler race would have certain advantages.

Sladen (1912, p. 142) speculated on the controlled breeding of bumblebees, and the hybridization of species. He suggested that the British race of *B. lapidarius* could be crossed with the more prolific races found in Europe, with the expectation that a breed would be obtained that would produce a much larger number of workers.



The absolute control of bumblebee mating is attainable by utilizing the technique of artificial insemination of the honeybee, described by Mackensen and Roberts (1948). Preliminary experiments were conducted by Medler and Hunt (Wis. Agr. Exp. Sta. Rept. 1950, unpublished).

A queen of *B. fervidus* was anesthetized with CO<sub>2</sub>. An examination of the genital organs showed that they resembled very closely those of the queen honeybee. A practice insemination with water was made. It was found that the syringe could be inserted with no leakage of water. It was concluded that artificial insemination of the queen bumblebee was possible provided that sperm could be obtained from the male.

An attempt to make a male of *B. fervidus* ejaculate by the same technique used for the male honeybee was unsuccessful. Ether was substituted for chloroform without results. The male was then dissected and it was found that its reproductive system was much different from that of a male honeybee. A storage organ for sperm was not discovered.

The artificial insemination experiments were postponed until a detailed study could be made of the reproductive organs of the male bumblebee.

The artificial insemination of queen bumblebees would enable a better degree of queen control in the fall than matings in cages or on tethers. Multiple insemination to provide more sperm also might be used to obtain a greater egg-laying capacity of queens, thereby increasing the number of worker bees available for pollination. With these and other possibilities in view, I believe that the breeding of bumblebees offers an interesting field for future research.

### POPULATION CONTROL

The study in nature of bumblebee colonies of each species has shown clearly that year to year fluctuations occur both in the number of colonies and the number of individuals in the colony. These wide variations in the population do not seem to be related to the colonial cycle of a species, i.e., nest foundation, production of workers, and appearance of the males and new queens; but rather to the bumblebees being victims of circumstances beyond their control. However it seems that some species under apparent optimum conditions produce smaller colonies than other species. These differences probably are explained on the basis of the high fecundity of queens of certain species and the different seasonal adjustments.

Populations are developed in relation to biotic factors, such as, (1), the inherent behavior pattern of the species, (2), queen vigor and (3), ratio of brood to workers. Major environmental factors are, (1) shelter, (2) food supply and (3) freedom from enemies. Cumber (1953) and Medler (1957) discussed some aspects of the biology and ecology of bumblebees in relation to populations.

In nature, the vigor of the queen foundress can be reduced by poor weather conditions during the hibernation period, or the premature emergence of the queen in the spring. Although the hibernation cycle of bumblebees seems to be linked closely with temperature and the phenology of flowering, an early spring followed by a prolonged period of cold, rainy weather can be detrimental. Also, a long winter may cause the queen to draw heavily upon her fat-body and emerge in a weakened condition. Some bumblebee queens will not be able to start nests because of nematode parasitism by *Sphaerularia bombi* (Duf.) which prevents the development of ovaries. Queen control as outlined previously should give uniformly vigorous queens.

Sladen (1899) first called attention to the two different groups of bumblebees: — the pocket-makers and the pollen-storers. The pocket-makers build little pouches or pockets on the sides of the larval cells, which receive the pollen gathered in comparatively small quantities. The pollen-storers accumulate pollen in cells which rise like columns and at times contain a large amount of pollen. Subsequent investigations by Plath (1934) showed that two American pocket-makers, *B. americanorum* and *B. fervidus*, will accumulate considerable quantities of pollen when colonies are prosperous and also at the time the young queens and males are reared. Cumber (1949a) discussed larval nutrition and the size of workers in relation to the pocket-making and pollen-

storing behavior of species. Further investigations of the different species should be made in order to determine if the pocket-making or pollen-storing habit can be associated with pollination efficiency.

A very important factor in the production and limitation of the worker population appears to be the food supply. A lack of suitable food during the pre-worker emergence period may reduce the number of workers. Plath (1934) reported that in a drouth year starvation caused a general lack of brood. On the other hand, it has been reported by Cumber (1949a) that an over-abundance of food results in a reduction of workers, because, if the food supply is increased disproportionately to the number of eggs laid by the queen the colony may change over to the production of sexual forms. Once the sexual forms appear the colony does not normally revert to the production of workers. Richards (1927) observed that bumblebees in sub-arctic regions, where there is a short but prolific flowering season, produce few workers. Cumber (1953) suggested that bumblebees in New Zealand may find in the exotic flowering plants a deep-seated supply of nectar for which there is little competition. In the major crop areas of North America the acreage of legumes has been greatly multiplied. Paradoxically it may be possible that the increase of nectar supplies by crop cultivation has resulted in bumblebees obtaining nectar with greater ease and efficiency, and consequently the colonies are changing from worker- to queen-production before they become populous. A critical study of these phenomena is basic to the population ecology of the bumblebee. In this connection it might be mentioned that valuable related information on the foraging and nesting biology of bumblebees has been published by Richards (1946), Cumber (1949a), Brian (1952) and Free (1955a, b, c).

The major environmental factors of a sheltered nesting situation and freedom of the colony from natural enemies should be largely controlled by the use of domiciles. Frison (1926b), Plath (1934) and Cumber (1949b) discussed the major parasites and predators of bumblebees. In Wisconsin, serious injury by enemies seems to be reduced in domiciled colonies, except that a small percentage of the colonies are attacked by *Psithyrus*. The establishment of parasite queens can be guarded against by a routine inspection of the colonies.

### CONCLUSION

The effective cross-pollination of crops by bumblebees will be possible when the basic facts of their biology and ecology are intelligently utilized in a practical system of management. Some principles and methods in rearing the colonies have been presented. But it also will be necessary that adequate numbers of workers of the most suitable species be made available at the time of flowering, and that the worker field force be maintained over the period of time necessary to accomplish pollination.

It is doubtful if the average grower will be in a position to cultivate bumblebees by the methods which I have outlined. Therefore, I envision a future need for trained personnel, appropriately called bombiculturists, who will be able to cultivate bumblebees for the business of pollination in a manner similar to the way honeybees are being used in certain seed growing areas today.

No doubt there will be some unforeseen difficulties encountered in the large-scale propagation of bumblebees, but such problems will be overcome by research, if the venture of bumblebee cultivation can be placed on a sound practical basis and be made interesting and profitable to the producer.

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# Bees, Their Relations to Melittophilous Plants and the Problem of Alfalfa Pollination<sup>1</sup>

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## ABSTRACT

*The parallel and dependent evolution of insects and Angiospermia is discussed. Specific instances of coadaptation of insects and plants are cited as well as cases where no morphological coadaptation exists between plants and the insects which pollinate them.*

At present more than 70 genera and 1200 species of bees are known to occur throughout Middle Asia, although their number is probably considerably greater. Studies of the relations of bees to plants in this area have just recently been initiated. Studies on the alfalfa pollinators indicated that it was necessary to know the pollinators of all the plants of the flora, but especially of leguminous plants. Since 1937, 75,500 bees have been collected in Uzbekistan, Tajikistan, Kirghizia and Kazakhstan, and their distribution over 320 species of melittophilous plants has been studied. The following results were obtained: feeding habits of many bee species were discovered; a number of mono-, oligo-, and polytropic species were revealed; the fauna of the Chenopodiaceae and alfalfa pollinators were ascertained.

The investigations made by the author and some scientists in Middle Asia and other regions of alfalfa seed production have shown that the part the honey bee plays in the alfalfa pollination is insignificant, while other bee species and genera are very important in this respect. The author considers that besides detailed studies of alfalfa pollinators selective work should be done to achieve the reciprocal adaptation of the honey bee and alfalfa, thus securing mass pollination.

The importance of insects in the evolution of Angiosperma is especially great and is generally well known. Their mutual evolution is one of the most brilliant parts of the modern theory of evolution.

However, the attempts to disclose the evolution of certain groups of melittophilous plants and of their bee-pollinators show that our knowledge is still exceedingly incomplete. Undoubtedly, the short-tongued forms are adapted for visiting non-specialized flowers, whereas the long-tongued ones are adapted for visiting the specialized long-tubed flowers.

We may state that the development of a long and sharply pointed proboscis among the lower, blunt and short-tongued forms, is a process of adaptation to nectar gathering from the melittophilous plants. It is independent not only in the various groups of Aculeata Hymenoptera as a whole but also, to a certain degree, in the different groups of the bees.

We may also ascertain that not only the development of the collecting apparatus but also that of abdominal brush are independent processes in different groups of bees as adaptations to the pollination of different melittophilous plants, i.e. for the collection of various types of pollen.

The processes of adaptation of the pollinators to the plants and vice-versa have, as a rule, a rather general character being independent and not connected with many morphological details. They are connected, however, with the physiological, phenological and other features as well as with the geographical distribution, habitat and behaviour of the bees.

However, there are cases of an exact mutual morphological, ecological and phenological adaptation of a monotrophic bee genus to a melittophilous plant (e.g. *Heriades* is adapted to *Campanula* and *Systropha* to *Convolvulus*, etc.)

But there are also some other cases in which a monotrophic bee-genus is exactly adapted in its ecology and phenology but not in its morphology to the plant it pollinates

<sup>1</sup>Also published in *Entomologicheskoe Obozrenie* 35(3):582-598. 1956. (Russian with English abstract).



Thus the species of *Macropis* which is spread through the central part of the Holarctic region visit the flowers of the two closely related genera of Primulaceae *Lysimachia* (Eurasia) and *Steironema* (N. America). Though interrelation of the plant and its pollinator is very close and old, the latter is morphologically not fully adapted to pollinate these flowers. A more close systematical and zoogeographical analysis of the bee, its parasite (*Epeoloides*) and the plants visited has shown that these relations are not the primitive ones.

Among the plants visited by the large *Xylocopa valga* Gerst. and *X. violacea* L. there are many southern and garden plants introduced into the Palearctic Region. These bees are better adapted to the pollination of other plants than the modern palearctic species. This corresponds well to the concept that the genus *Xylocopa* is a primitive wood dweller of the tropical and subtropical zones (Popov, 1947).

The leading importance of pollen collecting in the evolution of bees is beyond question. The natural selection is developed from the occasional consumption of pollen to the obligatory pollination of flowers and appearance of oligo- and monotrophic forms. This process was complicated and took a long period of time. Many of its details are still unknown and the evolution of certain groups now can hardly be understood, even in its outline. The study of these relations is especially complicated in the Holarctic, the youngest of the Regions; there is no doubt that many of the primitive interrelations were lost and replaced by other more recent ones.

The study of such primitive and modern interrelations of pollinators and plants, and their stability, as well as its clear understanding are of considerable interest from both theoretical and practical view-points.

There is no doubt that the majority of the entomophilous crop plants are practically pollinated or will be pollinated by the hive-bee (*Apis mellifera* L.). This is almost the only insect, the abundance and biology of which are entirely controlled by man. The part taken by the hive-bee in pollination is especially evident under more intensive agricultural conditions. The possibility of artificial pollination of flowers has also to be kept in mind. However, it has been practically proved, that neither the hive bee, nor artificial pollination are of value in alfalfa seed production.

As a preliminary to the study of alfalfa pollination it became necessary to investigate the bee-fauna of Middle Asia and of Kazakhstan and plants visited.

Many scientists have studied the constancy of the interrelations of the pollinators and the plants. However, the majority of them arrived at their conclusions after considering only single, or occasional observations of a few visits to the melittophilous plants alone, not taking into account the environment and the local bee-fauna as a whole.

It is well known that bees can be classified into three types: monotrophic species, each pollinating only one species of plant; oligotrophic species, which pollinate flowers of certain related groups of plants, and polytrophic species, which pollinate flowers of many different groups of plants. There exist many intermediate forms between the three groups mentioned above. The group of polytrophic bees exhibit the widest variety of pollinating habits, but even in this group there are no bees which visit all the species of melittophilous plants. Even the hive-bee, the most polytrophic species of all, does not collect nectar from all the local melittophilous plants. Observations carried out in Middle Asia have shown that in the same localities and in the same period of time *Andrena flavipes* Panz. visited 74 melittophilous plant species belonging to 26 families; the hive-bee visited 71 plants belonging to 27 families and could be found only on every 3rd species of the plants observed.

Robertson (1930) justly advised to be careful in considering either mono- or oligotrophic habits of any species, and indeed, the list of monotrophic and oligotrophic forms should be revised. This is especially true for the spring forms. It is possible that in the different parts of an area some species visit different species and genera of plants. The number of the mono- and oligotrophic forms is considerable. Thus for Alfken reports that  $\frac{1}{3}$  of bee species in N.-W. Germany are mono- and oligotrophic forms (Alfken, 1935).

The more important interrelations of the local bee fauna and the melittophilous plants should be investigated during the whole period of bloom. Such work was done

by Graenicher (1930, 1935) in Wisconsin and Robertson (1928) and Pearson (1935) in Illinois.

This method supposes not only recording of frequency of the visits to the plants but also the peculiarity of the bee work on them (pollen collecting, gathering of the nectar, etc.), as well as sex of the insect. In some cases the specific analysis of the collected pollen and the nectar quantity produced in the plant should be carried out.

This method of investigation illustrates the complete monotrophism of *Macropis* (see Table I).

TABLE I. *Macropis lobiata* Panz. as a Visitor of Melittophilous Plants in Janvarzevo, W.-Kazakhstan Region.

Plant visited		Period	Number	Number of bees collected during the flight period of the bee	Percentage of the same
Rosaceae:	Rubus caesius L.	29 VII 1949 20 VII 1950	2 ♀	74	4.0
Primulaceae:	Lysimachia vulgaris L.	21 VII 15 VIII 1949 11 VII 15 VIII 1950	108 ♀ /96p/ 5 ♂ 433 ♀ /367p/ 68 ♂	682	96.6
Compositae:	Inula britannica L.	24 VII 1949	1 ♂		
Alismataceae:	Alisma plantago-aquatica L.	16 VII 1950	1 ♂	119	0.8
		11 VII — 15 VIII	544 ♀ /463p/ 75 ♂	3290	

Its special preference to the flowers of *Lysimachia vulgaris* L. is evident, even though two females without pollen were found on *Rubus* flowers.

*Halictus nasicus* F. Mor. (Table II), as the two years observations in Tadjikistan and in Usbekistan showed, is an oligotrophic species visiting the flowers of Chenopodiaceae. It is interesting to note that different species Chenopodiaceae are of different attractiveness to *Halictus nasicus* F. Mor. and only one was recorded on the flowers of another family.

*Paranthidiellum cribratum* F. Mor. (Table III) is also an oligotrophic species, collecting pollen on Compositae (especially on *Onopordon* and *Pulicaria*), but the females may visit flowers of some other plant families. The list of melittophilous plants visited by males is still longer.

*Ceratina tibialis* F. Mor. (Table IV) is a limited polytrophic species. Its females were recorded on 24 melittophilous plants belonging to 9 families; pollen-collecting took place on the plants of 6 families, with some preference for Compositae flowers being evident.

Both *Andrena flavipes* Panz. and the hive-bee are of wide polytrophic habits.

When the problem of the bee-pollinators of alfalfa in the USSR was realized, there was almost no information on the interrelation of bees and melittophilous plants in Middle Asia and Kazakhstan.

The Hymenopterological Laboratory of the Zoological Institute, Academy of Sciences of the U.S.S.R. began these studies in Usbekistan, Kirghisia, Tadjikistan and Kazakhstan in 1937-1938.

TABLE II. *Halictus nasicus* F. Mor. as a Visitor to Melittophilous Plants in Middle Asia.

Plant visited	Place of observation	Period	Number		Number of bees collected during the flight period of the bee	Percentage of the same
Chenopodiaceae:	Halocharis hispida C.A.M.	Kurgan-Tubey, Tadj.	10 VIII — 6 IX 1948	640 ♀ 1020 ♂	4858	34.2
		S. Pristan, Tadj.	11 IX 1948	1 ♀	567	0.2
	Horaninowia ulicina Fish. et Mey.	Kurgan-Tubey, Uzb.	25 VII 1938	6 ♀	174	3.4
	Salsola dendroides Pall.	Kurgan-Tubey, Tadj.	11 VIII — 6 IX 1948	4 ♀ 649 ♂	709	90.1
Plumbaginaceae	Statice perfoliata Karel.	"	17 VIII 1948	1 ♂	263	0.4
25 VII — 11 IX				651 ♀ 1670 ♂	6571	

The observations were carried out in Djuma, near Samarkand (1937); in Kurgan-Tubey near Andijan (1938), where the fauna of the Fergana Mountains was also investigated. In 1943-44, and 1946-48 the investigations on the bee-fauna proceeded in the vicinity of Stalinabad, Kondara and Chodja-Obi-Garm (Hissar Mountains), in Kurgan-Tubey and Staraja Pristan (Valley of the river Vakhsh, South Tadjikistan). In 1949-51 the middle and lower parts of the Ural river (W. Kazakstan) were also investigated. 75,500 bees were collected and their interrelation with 320 melittophilous plants noted. Most of this material was studied, and partly published (Popov, 1952, 1954). The broad observations made it possible to ascertain the bee pollinators of alfalfa and their more or less close connection with this crop.

Among the Leguminosae already studied, the more important plants besides alfalfa are: *Cercis*, *Glycyrrhiza*, *Halimodendron*, *Indigofera*, *Lathyrus*, *Lotus*, *Melilotus*, *Prosopis*, *Psoralea*, *Sophora*, *Spartium*, *Trifolium*, *Trigonella*. To the list mentioned above the following species are peculiar to N.-W. Kazakstan: *Goebelia*, *Cytisus*, *Caragana*, *Astragalus*, *Vicia* and some others.

The majority of the species are widely spread plants of oases and cultivated lands. The main pollinators of these plants are also widely spread species in these districts. They are mostly polytrophic bees or oligotrophic species showing a preference for Leguminosae, Compositae and some other melittophilous plant families. The oases and cultivated land become attractive to the bee fauna of the surrounding territories, because there is a variety of melittophilous plants and more convenient places for the bee nesting sites.

The majority of mono- and oligotrophic species are of little or no value. On the other hand most of the polytrophic species are of great importance as crop pollinators.

The investigations of the Zoological institute in Middle Asia, the Caucasus and Kuban region proved 22 species out of 161 to be the main pollinators of alfalfa (Popov, 1951).

They are: *Halictus eurygnathus* Blüthg., *H. malachurus* Kby., *Andrena labialis* Kby., *A. flavipes* Panz., *A. albofasciata* Thoms., *Nomia diversipes* Latr., *Melitta leporina* Panz., *Melitturga clavicornis* Latr., *Megachile argentata* F., *M. pilidens* Alf., *M.*

TABLE III. *Paranthidiellum cribratum* F. Mor. as a Visitor of Melittophilous Plants in Middle Asia.

Plant visited		Place of observation	Period	Number		Number of bees collected during the flight period of the bee	Percentage of the same
Chenopodiaceae:	<i>Salsola transoxanana</i> Iljin	Kurgan-Tubey, Tadj.	21 VIII	—	1 ♂	199	0.5
Plumbaginaceae:	<i>Statice perfoliata</i> Karel.	"	21 VIII	—	1 ♂	263	0.4
Ranunculaceae:	<i>Clematis orientalis</i> L.	Kondara	6 IX	1 ♀	1 ♂	595	0.4
Leguminosae:	<i>Alhagi kirghisorum</i> Schr.	Stalinalbad	8 VIII	2 ♀	—	1867	0.1
	<i>Trifolium repens</i> L.	"	21 IX	—	1 ♂	24	4.2
Onagraceae:	<i>Epilobium hirsutum</i> L.	Kondara	5-12 IX	—	4 ♂	262	1.5
Dipsacaceae:	<i>Dipsacus lanceolatus</i> L.	Stalinalbad	4 VIII	1 ♀	—	77	1.3
Boraginaceae:	<i>Echium altissimum</i> L.	Djuma	31 V	—	2 ♂	122	1.6
Labiatae	<i>Mentha silvestris</i> L.	Stalinalbad	25 VIII-12 IX	1 ♀	2 ♂	1047	0.3
Verbenaceae:	<i>Verbena officinalis</i> L.	"	7 VIII-17 IX	1 ♀	2 ♂	144	2.1
	<i>Vitex agnus castus</i> L.	"	3 VIII	1 ♀	—	1079	0.1
Tamaricaceae:	<i>Tamarix</i> sp.	Kurgan-Tubey, Tadj.	3-20 VIII	—	2 ♂	1252	0.2
Compositae:	<i>Acroptilon picris</i> Pall.	Stalinalbad	13 VIII	1 ♀	2 ♂	96	3.2
	<i>Centaurea iberica</i> Trev.	"	25 IX	—	1 ♂	380	0.3
	<i>Cirsium turkestanicum</i> Reg.	Chodja-Obi-Garm	3 IX	1 ♀ /p/	—	149	0.7
	<i>Chondrilla juncea</i> L.	"	4 IX	1 ♀ /p/	—	83	1.2
	<i>Cynara scolymus</i> L.	Stalinalbad	3 VIII	1 ♀	—	34	2.9
	<i>Erigeron canadensis</i> L.	"	9-12 X	2 ♀ /p/	2 ♂	283	1.4
	<i>Inula</i> sp.	Kuirgan-Tubey, Tadj.	31 VIII	—	4 ♂	28	13.9
	<i>Matricaria desciformis</i> C.A.M.	Stalinalbad	19 V	—	1 ♂	167	0.6
	<i>Onopordon acanthium</i> L.	"	25 VIII-22 IX	23 ♀ /17p/	—	293	7.8
	<i>Pulicaria salviaefolia</i> Bge.	"	15 VIII-30 IX	28 ♀ /17p/	34 ♂	331	21.1
19 V — 30 IX					74 ♀ /38p/	60 ♂	8775

TABLE IV. *Ceratina tibialis* F. Mor. as a Visitor of Melittophilous Plants in Middle Asia.

Plant visited		Place of observation	Period	Number		Number of the bees collected during the flight period of the bee	Percentage of the same
Ranunculaceae:	<i>Clementis orientalis</i> L.	Kondara	8-12 IX	4 ♀	2 ♂	595	1.0
Leguminosae:	<i>Alhagi kirghisorum</i> Schr.	Stalinalbad	3 VIII	2 ♀ /p/	—	1867	0.1
	<i>Cercis siliquastrum</i> L.	"	29 IV	—	1 ♂	116	0.8
	<i>Indigofera Gerardiana</i> Wall.	"	13 VII	1 ♀	—	124	0.8
	<i>Medicago sativa</i> L.	"	25 VIII	1 ♀	—	487	0.3
Onagraceae:	<i>Epilobium hirsutum</i> L.	Kondara	5-15 IX	30 ♀ /3p/	5 ♂	262	13.4
Umbelliferae:	<i>Eryngium coeruleum</i> MB.	Stalinalbad	29 VI-10 VII	2 ♀ /1p/	2 ♂	522	0.8
Dipsacaceae:	<i>Dipsacus laciniatus</i> L.	"	4 VIII	2 ♀	—	77	2.6
Boraginaceae:	<i>Echium italicum</i> L.	"	23 VI-13 VII	2 ♀ /1p/	—	9	—
	<i>Heliotropium</i> sp.	"	15 VIII-7 IX	2 ♀	1 ♂	225	1.3
Labiatae:	<i>Hyssopus officinalis</i> L.	"	8 VI	2 ♀	1 ♂	478	0.6
	<i>Ocimum basilicum</i> L.	"	7-10 X	5 ♀	—	1158	0.4
	<i>Salvia officinalis</i> L.	"	27 V-3 VI	3 ♀	3 ♂	265	2.3
Verbenaceae:	<i>Verbena officinalis</i> L.	"	24 VIII-26 IX	10 ♀	1 ♂	153	7.2
		Kondara	15 IX	1 ♀	1 ♂	8	—
Cruciferae:	<i>Sisymbrium Loeselii</i> L.	Stalinalbad	1 VIII	1 ♀ /p/	—	42	2.4
Compositae:		Kondara	13 VII	1 ♀	—	1	—
	<i>Centaurea iberica</i> Trev.	Stalinalbad	13 VII-13 VIII	6 ♀	/3p/	380	1.6
	<i>C. solstitialis</i> L.	"	20 VI-1 VIII	18 ♀ /4p/	3 ♂	955	2.2
	<i>C. squarrosa</i> Willd.	Chodja-Obi-Garm	29 VIII	1 ♀ /p/	—	306	0.3
	<i>Chondrilla juncea</i> L.	Kondara	5-14 IX	20 ♀ /3p/	5 ♂	151	16.5
	<i>Erigeron canadensis</i> L.	Stalinalbad	24 IX-9 X	3 ♀	2 ♂	289	1.7
	<i>Onopordon acanthium</i> L.	"	24 VIII-21 IX	5 ♀	1 ♂	289	2.1
		Kondara	16 IX	1 ♀	—	11	9.0
	<i>Pulicaria salviaefolia</i> Bge.	Stalinalbad	12-19 IX	3 ♀	—	331	0.9
29 IV — 10 X				126 ♀ /19p/	26 ♂	9101	



*maritima* Kby., *M. saussurei* Rad., *Eucera tuberculata* F., *E. interrupta* Baer, *E. clypeata* Erichs., *E. nigrifacies* Lep., *E. chrysopyga* Pér., *Tetralonia tricineta* Eversm., *Amegilla magnilabris* Fedt., *Bombus silvarum* L., *B. agrorum* F., and *B. terrestris* L.

The number of the females from the above species varied in different localities from about 75.5 to 96% of all the females recorded.

Many of these species of bees, as well as a few others, have been cited by authors listed in an earlier paper (Popov, 1951). Some new data on the subject are given in the following papers. Rymashevskaya (1951, 1952a, 1952b) records *Melitta leporina* Panz., *Andrena albofasciata* Thoms., *A. flavipes* Panz., *Megachile argentata* F. and a number of others to be the main pollinators of alfalfa in Alma-Ata region.

According to L. S. Pachina the main pollinators of alfalfa in East Kasakstan region are *Melitturga clavicornis* Latr., *Melitta leporina* Panz., *Andrena flavipes* Panz. and many of *Halictus* species. Alfalfa pollinators near Tashkent (Burnacheva, 1954) are species of *Andrena* and *Megachile*. Six dissertations for the degree of "Candidate of Biology" were recently written on the problem of alfalfa pollination and its pollinators in Kasakstan (Rymachevskaya, 1952b), the Volga region (Panfilov, 1952, Juravlev, 1953, Pisarev, 1953, Blagovestchenskaya, 1954) and in the Voronezh region (Zavgorodnaya, 1952), which confirmed the important role of the wild bees in alfalfa pollination.

The alfalfa pollinators were also studied in S.W. Ukraina (Osychnuk, 1955). Among the 60 species found there, the following bees were recorded: *Andrena flavipes* Panz., *Andrena albofasciata* Thoms., several *Halictus* species, *Megachile argentata* F., *Eucera clypeata* Er., *Nomia diversipes* Latr., *Melitturga clavicornis* Latr., and *Melitta leporina* Panz. The alfalfa pollinators in the Stalingrad region were mentioned by Nefedov (1953) and Detkova (1954); they mention 22 species, and *Melitta*, *Nomia*, *Melitturga clavicornis* Latr., and *Andrena* are among them.

The greatest part of the alfalfa seed producing territory of the U.S.S.R. was under investigation.

As the result the importance of wild bees in alfalfa pollination was evident while the hive-bee is of very little value. This is in concordance with the latest data obtained abroad. Linsley (1946), Hobbs and Lilly (1954), Stephen (1955) discuss the problem recording the previous investigations.

There are some records on alfalfa pollinating by the hive-bee. The test data on this subject were given by Ponomarev (1954). Not all of the investigations recorded are reliable. Nevertheless, it seems probable, that when lack of pollen occurs the hive-bee, as an exception, will pollinate alfalfa.

When the nectar production increases, a considerable number of hive-bees may be found on alfalfa and they even pollinate a few flowers; in this case the percentage of pollination varies from one tenth to 6% (Bogojavlensky, 1951; Rymachevskaja, 1951, 1952). Higher percentages have not been confirmed.

Wild bee accumulation on the alfalfa seed plots presents a new problem to solve.

Some authors recommend mowing the weeds surrounding alfalfa seed plots as well as cutting the rest of alfalfa field in some sequence.

Alfalfa seed-plots, as the practice shows, should be small and chosen near uncultivated areas like gullies, steep slopes, ravines, roadsides and some other favourite bee-nesting sites. The pollinators accumulate and their colonies grow larger in such places from year to year.

Many bees form colonies which exist for years. A colony of *Melitturga clavicornis* Latr. in Germany existed for 100 years. Some colonies of *Andrena* in England have been known for more than 40 years. The size of such a colony is immense. Thus, the colony of *Rophites canus* Eversm. (one of the main alfalfa pollinators in the Ulianov region) occupied about 64 sq.m. and contained more than 5000 nests (Blagovestchenskaja 1954b; 1955a).

A well chosen place for the alfalfa seed plots can provide a considerable increase in seed production, as was demonstrated by some experiments by Melnitchenko, in 1953.

Artificial places for bee-nesting sites were suggested. Juravlev (1953) tried to use this idea in his tests with *Megachile* but only 11.6% of the nests became inhabited.

In spite of the importance of the wild bees in alfalfa pollination, it is still necessary to continue the studies on the hive-bee as a pollinator of alfalfa. There is no doubt that selective work should be done in the mutual adaptation of the hive-bee and alfalfa flowers.

A method of inducing bees to feed on alfalfa has not been perfected. The results to date show only an increase in honey production in the bee hives.

The training of bees to visit alfalfa flowers combined with a provoked lack of pollen in the hive, do not make hive bees collect alfalfa pollen. As shown by Blagovestchenskaya (1955), bees collect pollen on flowers of *Berteroa*, *Fagopyrum*, *Melilotus*, *Sisymbrium*, *Trifolium*, *Phacelia*, *Salvia* and *Compositae*. A careful analysis of the pollen as a rule is not done, though it is quite necessary.

The methods of artificial pollination of alfalfa are various. A special mechanism was constructed for this purpose, but careful examination of all these methods of pollination showed them to have no effect upon alfalfa seed production (Burnacheva, 1954; Blagovestchenskaya, 1955a).

There are numerous ways in which the alfalfa seed problem may be solved. Only two of them are of importance to the entomologist: 1. Alfalfa and hive-bee selection in the direction of reciprocal adaptation to pollination. 2. Complete and absorbed studies of wild bees as the only real alfalfa pollinator.

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# Improved Methods of Determining Diastase and Hydroxy-Methyl-Furfural in Honey and Their Relationship to the Bacteriostatic Quality of Honey

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## ABSTRACT

Photoelectric colorimetric methods of measuring diastase ( $\alpha$ -amylase) and hydroxy-methyl-furfural (HMF) were devised to replace the more subjective color tests used for routine analysis of honeys. The simplicity and precision of the new methods, both of which employ a Klett-Summerson photoelectric colorimeter, recommend them for official analysis.

A large variation was found in the diastase content of fresh, unheated honeys of different pH values. The rate of loss of diastase during a given heat treatment varies among honeys and apparently is related to the pH value of the honey. Moisture content was found to be an important factor in the rate of formation of HMF in a given honey. However, the rate of formation of HMF was found to vary among several honeys having similar pH values and moisture contents.

The rate of loss of diastase in an alfalfa honey was found to increase more appreciably with temperature than the rate of formation of HMF, so that at 160°F. (71°C.) the diastase became very low before HMF could be detected with the Fiehe test. On the other hand, storage of several honeys at 70°F. for one year resulted in little change in their diastase activities, but increased the HMF sufficiently to change their Fiehe Reaction.

Several alfalfa honeys were found that failed to meet the requirements for "unheated honeys" but which, nevertheless, contained appreciable amounts of a heat labile bacteriostatic factor ("inhibine"). This factor is more sensitive to temperatures of 50-70°C. than diastase in honey of pH 3.5.

Honeys are labeled as adulterated in Germany if they do not meet the requirements of the German honey regulations regarding diastase activity and hydroxy-methyl-furfural. The diastase activity of natural honey is rapidly reduced when honey is heated (Auszinger, 1910; Gothe, 1914; Lampitt *et al.*, 1929; Kiermeier and Köberlein, 1954) or stored at unfavorable temperatures. A very low diastase activity allegedly indicates that the honey has been subjected to unfavorable temperatures (Gothé, 1914). Similarly, the presence of an appreciable amount of HMF has been interpreted as evidence of alteration of the honey by heat. Gothe's suggestion that the Fiehe test for HMF should be used in conjunction with the diastase assay in judging a honey of low diastase activity has evidently become a rule in the control laboratories of Germany (Duisberg, 1955).

According to the German honey regulations, any alteration or change in the composition of natural honey is to be considered an adulteration. In addition, high HMF content and a lack of diastase are characteristic of artificial honeys. Heating to a very high temperature is believed to destroy certain dietetic values of honey (Kiermeier and Köberlein, 1954). Furthermore, honey has been shown to have a certain amount of "bacteriostatic ability" other than that due to its sugar and acid content (Dold, Du, and Dziao, 1937; Prica, 1938). This bactericidal quality, which Dold and coworkers referred to as "inhibine", is heat labile (Dold *et al.*, 1937; Prica, 1938; Plachy, 1944; Pothmann, 1950). At present the sensitivity of this inhibine to heat seems to be a major reason, although still not the only reason, for the undesirability of heated honeys under the German standards.

Both the diastase test and the HMF test are simpler, much more rapid, and less expensive to make than the biological analysis for inhibine. However, diastase activity

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varies greatly among honeys of a given floral source. Because of this variation and because of the difficulties involved in obtaining easily reproducible assays, there have arisen numerous doubts concerning the validity of the regulations of the German Food Control regarding the amount of diastase that must be present for a honey to be considered unheated (Kiermeier and Köberlein, 1954). Similarly with HMF, Lampitt and Rooke (1929) reported their inability in most cases to detect the overheating of honey with the Fiehe reaction before the flavor had been noticeably impaired. Obviously it was necessary to devise more precise and reproducible methods before dependable studies could be made of the natural occurrence of these substances in unheated honeys and of the effect of heat on such substances. When this was accomplished the relationship of the diastase content and the HMF content to the bacteriostatic quality of honey was then studied.

## METHODS AND MATERIALS

Honey samples were collected over a period of two years from the California producers and honey buyers, an attempt being made to secure unheated samples in liquid or granulated form. Some samples were drained from the comb and still others were obtained by different processes used in the normal practices of extracting honey. Some samples were stored at 20° C. for extended periods, while others were exposed to higher temperatures for specified intervals.

A modification of the method of Schwimmer (1947) for determining diastase activity of barley malt was used in the present studies. This modified method employs a Klett-Summerson photoelectric colorimeter to measure the time required for a given amount of honey to decompose a given amount of starch to a prescribed endpoint. The time required to reach the endpoint is indirectly proportional to the diastase activity.

The concentration of HMF in honey samples was estimated by a modification of the Fiehe test that used a Klett-Summerson photoelectric colorimeter to measure objectively the intensity of the Fiehe reaction. The results obtained with this method were compared with the more subjective estimation of HMF by the visual Fiehe test, as described and illustrated to the authors personally by Dr. H. Duisberg, Leiter des Instituts für Honigforschung in Bremen, Germany. Both procedures used standardized methods for the extraction of HMF with anhydrous ether.

The bactericidal quality of honey samples was estimated by a modification of the method proposed by Dold and Witzenhausen.<sup>2</sup> Dold and Witzenhausen used a haematin-agar (blood agar) medium, which is troublesome to prepare. Furthermore, their method involved a variation in the concentration of the agar medium in addition to the desired variation of the concentration of honey; with this variation of nutrients some differences in growth could be expected even in the absence of honey. The procedure used for the present work has overcome these difficulties and also embodies several simplifications in the manipulations of the assay. In addition the series of concentrations of honey has been changed somewhat; instead of a series of 5 plates of concentrations between approximately 5% and 25%, a series of 5 plates of approximately 4% to 21% was used. Inhibition that occurs at a concentration of about 25% honey is difficult to distinguish from that due to sugar and acid constituents of honey. It seems best to disregard such a slight inhibition, since it certainly is of doubtful significance. The use of the same number of plates for a smaller range of concentrations has a slight advantage in detecting small differences in inhibine value.

A constant amount of nutrient agar (Difco) of double the strength normally used for media was mixed with a constant amount of each solution of a series of five dilutions of a honey. The five dilutions of each honey were prepared from a solution consisting of 25 grams of honey dissolved in 25 ml. of sterile water in a sterile, wide-mouth jar. The dilutions were made in sterile test tubes in the manner shown in Table I.

After bringing the nutrient agar into solution the medium was cooled to 62.5 C. in a thermostatically controlled water bath, and while at this temperature 15 ml. aliquots of the medium were pipetted into screw-cap vials of about 50 ml. capacity. The vials of media were autoclaved for 15 minutes at 15 pounds pressure. As needed the tubes

<sup>2</sup>Information concerning this method was provided by Dr. H. Duisberg.



TABLE I — Dilutions Made and the Corresponding Concentration of Honey in the Final Plates of Agar Medium.

Tube No. (Plate No.)	Volume of Honey Solution ml.	Volume of Sterile Water ml.	Approx. Conc. of Honey in Final Agar Medium, o/o
1	10	3	21.3
2	8	5	17.3
3	6	7	13.1
4	4	9	8.9
5	2	11	4.5

of agar were re-liquified and cooled to 50 C in a thermostatically control water bath. The solutions of a single honey were warmed in a 40 C bath for 3-5 minutes. The entire 13 ml. of each honey solution was added to a vial of the liquid nutrient agar, the contents were mixed by inverting the screw-capped tube 6 to 7 times, and approximately equal amounts of the mixture were added to each of two Petri dishes of 8 cm. diameter.

Each plate was inoculated with 0.1 ml. of a sterile water suspension of *Micrococcus aureus* var. *pyogenes* (*Staphylococcus aureus*)<sup>3</sup> prepared from a 20-30 hour culture grown on a slant of nutrient agar at room temperature. The suspension consisted of approximately 9 ml. of sterile water and 0.1 ml. of an initial suspension consisting of a small loopful of the organism suspended in about 9 ml. of sterile water. The inoculum of each plate was spread with the aid of a sterile glass rake. The growth was observed and recorded after 20-24 hours incubation at 35° C and sometimes again after further incubation.

A few large colonies, distinctly different from those of the test organism, were often observed on the plates of lower concentrations of honeys. These colonies were ignored in evaluating the results.

The growth on the plates was recorded in the following manner: (1) good growth over all or most of the plate, ++; (2) sparse growth—ie., weak growth over most of the plate, +; (3) no bacterial growth, —; (4) only a few colonies on a small portion of the plate, e.g., less than 25 colonies, some of which may be contaminants from the honey, —; (5) 25 to 100 colonies on a small portion of the plate, + —. More precise readings were deemed unnecessary for the present work, and, furthermore, were not warranted with the procedure described.

The inhibine value is determined from the plate of lowest honey concentration that shows an inhibition of growth of the test organism. The inhibine value is arbitrarily assigned the number of the plate as shown in Table I. For example, a honey showing complete inhibition of growth at about 8.9 per cent concentration is assigned an inhibine value of 4; if instead of complete inhibition the same plate showed sparse growth or only a trace of growth (+ or + —), the inhibine value would be somewhat less than 4, e.g., 3.5 or 3.7, respectively.

## RESULTS AND DISCUSSION

The photometric methods used in the present work for determining diastase activity and HMF were compared with the classic methods of Gothe and Fiehe in a recent presentation at the International Beekeepers Congress in Vienna, Austria (August, 1956). The results of the work reported in Vienna showed that diastase activities obtained by a modified Gothe method and the present method are roughly comparable, although the latter assay procedure is more precise. Similarly, the photometric measurements of the concentration of HMF in the ether extracts of several honeys were compared with the readings obtained for the Fiehe tests. The results indicate that a concentration of approximately 8 to 10 micrograms or more of HMF

<sup>3</sup>Two strains of *Staph. aureus* that has been isolated from spoiled food were used for the work. Both strains gave identical inhibine values at first. Later a slight difference in sensitivity of the two strains to several honeys was observed, but the difference was always within one inhibine unit. The lower-most inhibine value was used in the summary of results. The less sensitive of the strains was used alone for later studies.



per gram of honey is necessary to get a positive Fiehe reaction, depending on the amount of interfering substances that often confuse the qualitative reading. The objectivity and greater precision of the present methods have enabled a better comparison of the rates of change of diastase and HMF among honeys heated or stored in the same manner.

The results also support the contention that diastase activity varies too greatly among honeys to be a good index of heat treatment by itself. [For further discussion of usefulness of diastase assays see Kiermeier and Köberlein (1954)]. In a series of 12 samples examined in the above work the diastase varied from 27.5 to 4.0 units per gram of honey, the latter activity being obtained for a sample of orange honey drained from its comb.

In addition to the natural variation of diastase in fresh honeys, Kiermeier and Köberlein (1954) report that a variation of sensitivity of diastase to heat occurs among honeys and conclude that this variation is due to the difference in pH. Our work with several honeys of different pH values tends to support the conclusion of Kiermeier and Köberlein, although the number of samples examined by us was admittedly few. The precision of the new photometric determination is illustrated by the data obtained

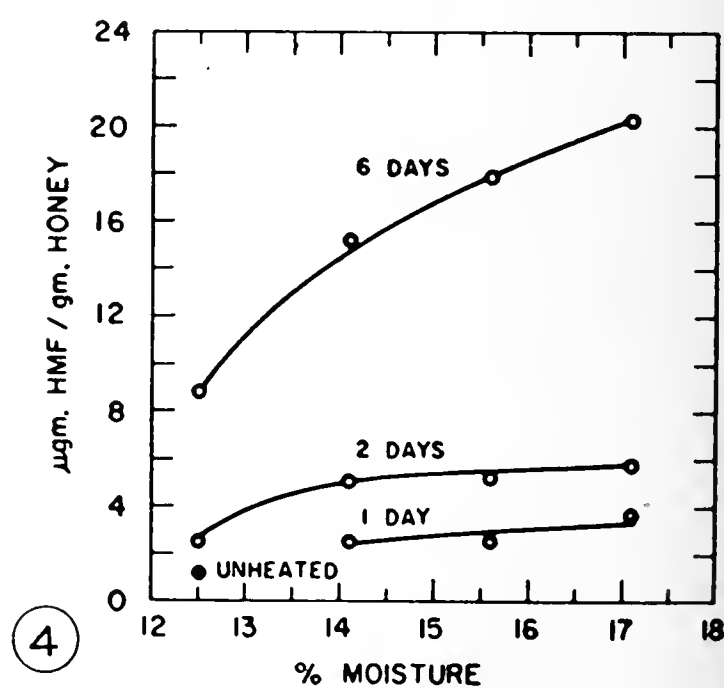
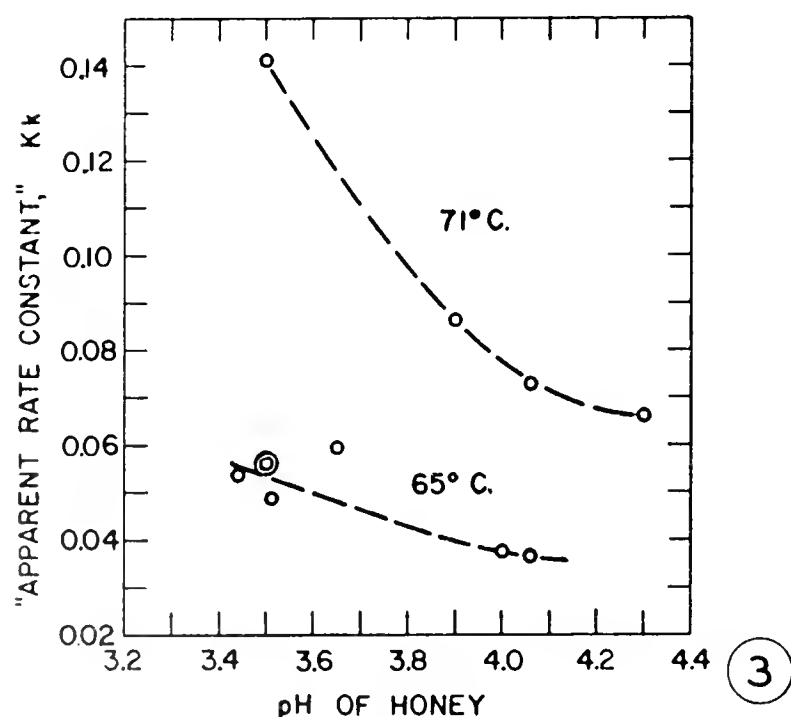
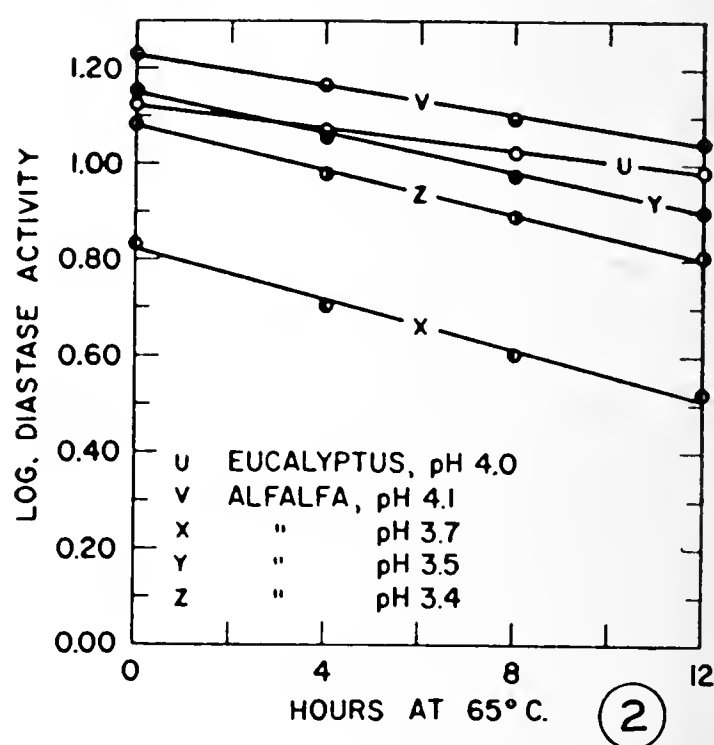
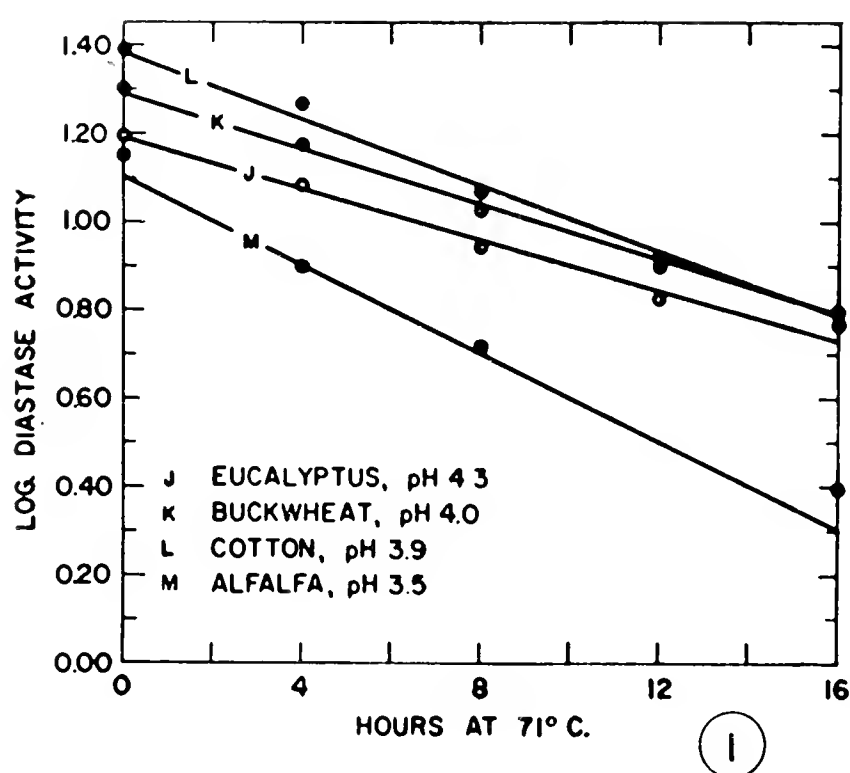


Fig. 1. Inactivation of diastase in honeys heated at 71°C.

Fig. 2. Inactivation of diastase in honeys heated at 65°C.

Fig. 3. The relationship of pH of honey to the rate of inactivation of diastase in honeys heated at 65° and 71°C.

Fig. 4. The effect of moisture content on the rate of HMF formation in a single alfalfa honey heated at 55°C.

for the decrease in diastase activity during given heat treatments. Since the diastase activity is proportional to enzyme concentration, a plot of the log of the diastase activity versus time of heating should give a straight line if First Order kinetics are involved in the inactivation. As shown in Figs. 1 and 2 First Order kinetics are demonstrated quite consistently for the samples analyzed. The alfalfa honey (Sample M) in Fig. 1, which showed the greatest rate of inactivation, was further heated at 3 other temperatures (see Fig. 6) and from this data an Arrhenius-type plot was made to relate the rate of inactivation to temperature.<sup>4</sup>

The Arrhenius plot is useful for estimating the rate of inactivation at temperatures intermediate of those employed. For example, the "apparent rate constants",  $kK$ , for the inactivation of the diastase at 71° C. and 65° C. were calculated from the curves in Figs. 1 and 2 and were plotted against pH to determine the effect of pH on inactivation (see Fig. 3). Although honey sample M was not heated at 65°, its apparent rate constant for 65° C. could be calculated from the Arrhenius plot in Fig. 6; the calculated  $kK$ , as shown in the double circle in Fig. 3, falls within the range of values obtained for the honeys of similar pH. The results in Fig. 3 further illustrate that the increase in rate of inactivation with increase in temperature from 65° C to 71° C is greater for honeys of low pH than those of high pH. Thus, the above data seem to substantiate the hypothesis that the sensitivity of diastase varies among honeys because of differences in pH.

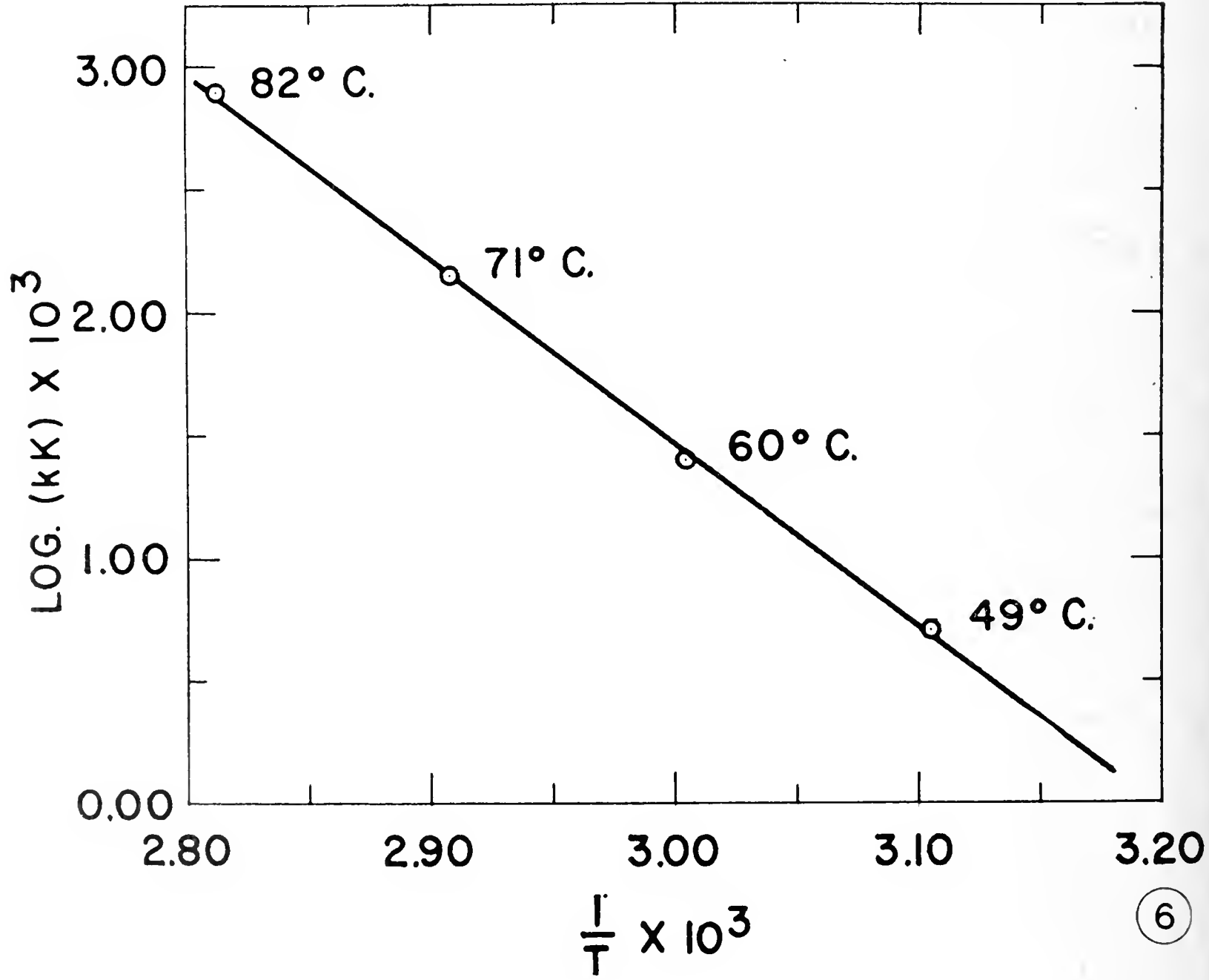
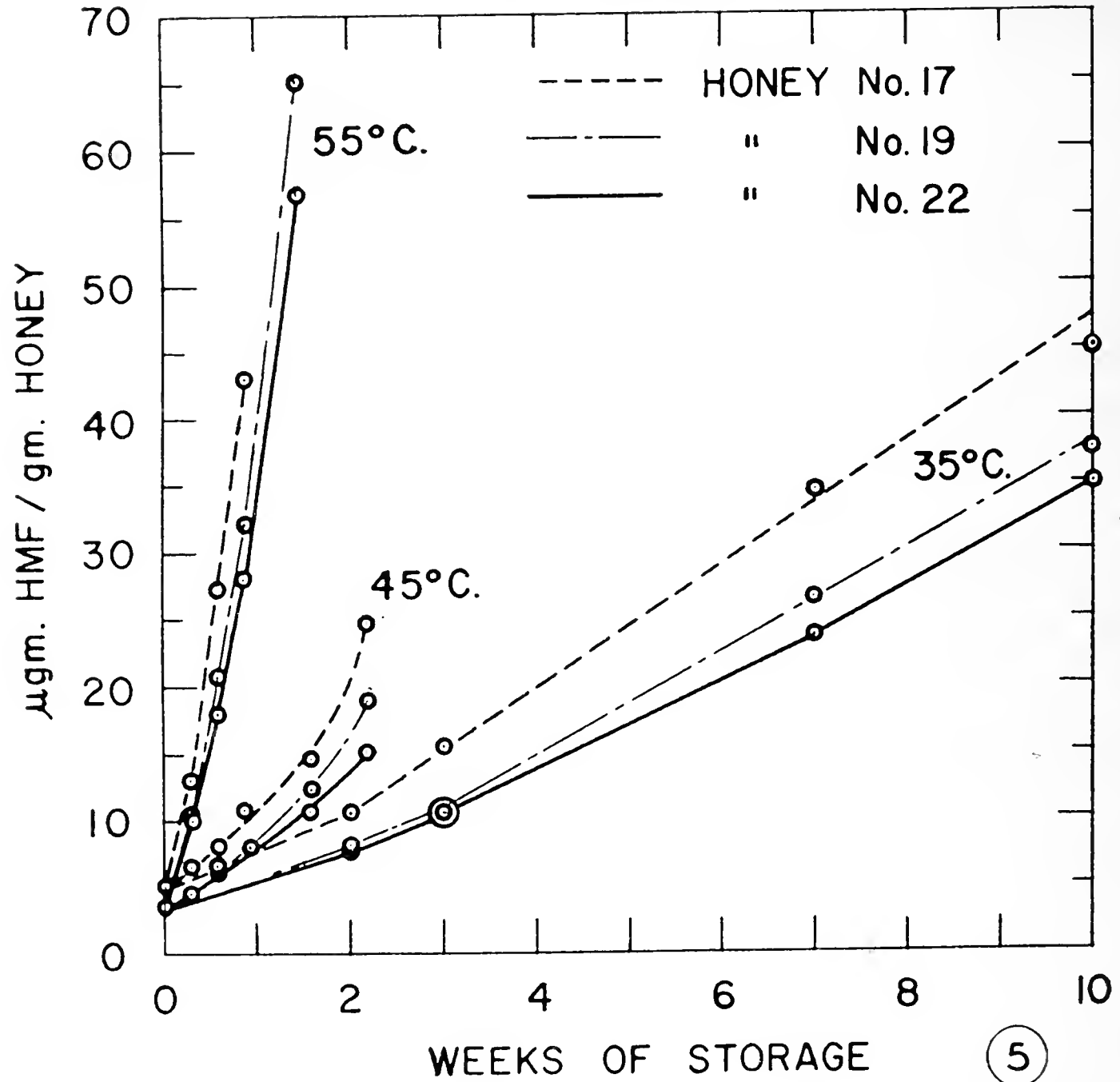
The rates of formation of HMF in three alfalfa honeys were compared using the photometric method of measuring the Fiehe reaction. These three honeys, which had similar moisture contents (16.6, 16.6, 16.1), similar pH values (3.7, 3.6, 3.7), and no appreciable amount of HMF, were stored in incubator rooms at 35° C, 45° C, and 55° C after bringing the samples to the desired temperature in a water bath. As shown in Fig. 5, the rates of forming HMF varied measurably among these honeys, although the differences were not great until the heat treatments were prolonged and objectionable amounts of HMF had been produced. Since relatively high temperatures are commonly reached in some parts of California, it is quite possible to get detectable amounts of HMF formed by comparatively short exposures to such temperatures.

As may be noted from Fig. 5, the rate of forming HMF is low at first and increases as the concentration of HMF increases. Some preliminary experiments with honey sample M indicated that at high temperatures (71°-82° C) the diastase activity could be greatly reduced before a positive Fiehe reaction would be obtained. However, such initial heat treatments seemed to be sufficient to accelerate the formation of HMF during storage at 20° C., so that the Fiehe reaction often became positive after several weeks of storage. Even samples heated at 60° C. for 12-16 hours, which previously showed comparatively little loss of diastase and gave negative Fiehe reactions, were found to give positive reactions after storage for 9-10 weeks. Unheated samples, on the other hand, showed no change in this period.

A very important factor influencing the rate of HMF formation appears to be the moisture content. Samples of a single white alfalfa honey (approximately 12.5% moisture content) were diluted with increasing quantities of distilled water to moisture contents ranging up to 17.2%. These samples were then heated at 55° C for 1, 2, and 6 days. The moisture contents were determined with an Abbé refractometer before and after the heat treatments. As usual 5.00 grams of the samples were extracted with ether for the analysis. The concentration of HMF was calculated from the assay for the weight of the original honey represented in 5.00 grams of the adjusted samples. The amount of HMF formed in 6 days increased notably with increase in moisture, as shown in Fig. 4. The difference was much less marked in the less severely heated samples. Thus, it has been shown that the rate of forming HMF as well as the rate of losing diastase may vary greatly among different honeys.

The work discussed here clearly indicates that the rates of change in HMF and diastase may be expected to vary greatly among honeys treated in similar fashion in

<sup>4</sup>The actual rate constants,  $k$ , for the inactivation of diastase are not obtained from the slopes in Figures 1, 2 and 3, since enzyme activity is used in place of enzyme concentration. However, the slope of each line multiplied by 2.3 will give an "apparent rate constant" for inactivation that is equal to the actual rate constant,  $k$ , multiplied by a constant quantity,  $K$ , that may be defined as a proportionality factor relating enzyme concentration to enzyme activity.



respect to heat and storage. In view of such variation it seems likely that the establishment of minimum diastase contents or maximum HMF contents could discriminate against certain honeys that are heated to no greater extent than others found acceptable under such standards. The relationship of the nutritious values of honeys to such standards remains to be studied. With the latter question in mind a few preliminary examinations were made to compare the bactericidal quality (inhibine values) of honeys that did and did not meet the present rule for judging honey employed by the Instituts für Honigforschung in Bremen, Germany. The Fiehe reaction and/or HMF contents of "acceptable" and "unacceptable" honeys are compared with their inhibine values in Tables II and III. Honeys in Table II have too large amounts of HMF for their comparatively low diastase activities to meet German standards. Nevertheless, honey No. 57 which had considerable amounts of HMF gave the maximum inhibine value for the present procedure. Not even the acceptable honeys examined in Table III showed such a strong inhibitive action. Furthermore, this inhibition was shown to be due to a heat labile factor, since the inhibition was lost completely when the 50-50 solution of honey was heated in a boiling water bath for 15-20 minutes. It seems noteworthy that in both tables the samples showing the somewhat lower inhibine values (3 to 0) were from the older honeys. Also, it should be noted that the buckwheat honey (Table III) showed little inhibine activity in spite of its high diastase content, which had decreased by only 1.4 units during 15 months of storage at 20° C. previous to the above analysis.

The results with honey sample M in Table III indicate that the inhibine is more sensitive than diastase to high temperatures. This observation is supported by data

TABLE II — The "Inhibine Values" of Several Honeys that Fail to Meet the German Regulations for Diastase and HMF.

No.	HONEY	FIEHE REACTION	HMF Quantitative Fiehe Method (μgm./gm.)	DIASTASE (units/gm.)	INHIBINE	
					Assay	After heating honey sol'n.
9	Alfalfa, 1955	+ -	9.0	6.7	4.0	
10	Alfalfa, 1955	+	13.0	6.9	4.0	10
55	Alfalfa, 1955		15.0	4.5	4.0	
57	Alfalfa, 1955		18.0	6.7	5.0	0.0
58	No. 57- liquid		33.0	trace only	0.0	
Q	Alfalfa, 1954	+++	—	7.3	3.0	
5 <sub>x</sub>	Orange, 1954	+	—	5.2	0.0	
7 <sub>x</sub>	Alfalfa, 1954	+	—	7.4	1.0	

Fig. 5. Formation of HMF in three alfalfa honeys during storage at elevated temperatures.  
Fig. 6. An Arrhenius-type plot showing the effect of temperature on the loss of "diastase activity" in an alfalfa honey (pH 3.5).

TABLE III — The "Inhibine Values" of Several Honeys that Apparently Meet the German Regulations for Diastase and HMF.

No.	HONEY	FIEHE REACTION	HMF Quantitative Fiehe Method ( $\mu\text{gm/gm}$ )	DIASTASE (units/gm.)	INHIBINE	
					Assay	After heating honey sol'n.
20	Alfalfa, 1955	—		17.1	4.0	1.0
M	Alfalfa, 1954	—	4.5	12.5	4.0	
M*	No. M, heated*		7.0	9.5	0.5	
4 <sub>x</sub>	Buckwheat, 1954	— +		26.1	0.5	
10 <sub>x</sub>	Alfalfa, 1954	+		21.6	2.5	

\* Heated over a 3 hour period to 71° C.

obtained with honey No. 57 that was heated at 62.8° C. (145° F.) for 0, 1, and 4½ hours. The results given in Table IV show that the inhibine is reduced considerably during heating, while the diastase changes only slightly.<sup>5</sup>

TABLE IV — A Comparison of the Effect of Heat (62.8°) on Inhibine and Diastase in Honey Number 57. Stored for 18 Days Before Analyzing.

TREATMENT	INHIBINE VALUE	DIASTASE units / gm.
UNHEATED	5.0	6.7
0 HOUR 15 MIN. PREHEATING	4.5	
1 HOUR	3.0	
4 ½ HOURS	2.3	5.4

If the inhibine is more sensitive to heat than diastase, the honeys in Table II having high inhibine should not be judged as unacceptable because of overheating. Certainly the search for better methods of judging the acceptability of a honey should be continued with both a desire for a simple method and for a method that allows uniform judgment.

<sup>5</sup>A severe overheating of a honey or a honey solution results in degradation products that retard the rate of bacterial growth. That such a treatment must be severe is shown by the fact that a honey (No. 22) showing an inhibine value of 3 lost all inhibitive action after heating for 15 days at 130° F. although at this time it contained at least 84  $\mu\text{gm}$  of HMF per gram of honey.



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# Maltose Content of Canadian Honeys and Its Probable Effects on Crystallization

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## ABSTRACT

*Thirty-six Canadian honeys, selected as being typical of the major producing areas, were analysed by A.O.A.C. polarimetric procedures and by the selective adsorption method of White and Maher. Analyses by the latter method indicate relatively large amounts of reducing disaccharides (as maltose) in all honeys tested. The effect of this sugar on the crystallizing potential of honey is discussed. An identification of pollen, in each of the honeys, was made to determine floral derivation.*

## INTRODUCTION

Until recently, most Canadian honey appeared on the market in the recrystallized form. However, liquid honey is not only intrinsically more appealing to many consumers but lends itself more readily to packaging in the smaller and more attractive containers currently in vogue in competitive trade. Thus more and more liquid honey is being packed each year.

In the course of exploring methods whereby liquid honey could be maintained crystal-free for reasonable periods of time, samples were gathered from most of the major producing areas across Canada. Most of the samples were submitted by the various honey co-operatives and were selected because they typified the honey produced in certain regions within the respective provinces. Our intention was to analyse the samples and, on the basis of their levulose-to-dextrose (L/D) ratios, provide a guide for selecting honeys for packing in the liquid form.

White *et al.* (1952), made a comprehensive comparison of methods currently in use for determining levulose and dextrose in honey. After statistically analysing the results from five analytical methods they concluded that variance due to methods was as great as that due to differences in dextrose and levulose content of samples from fourteen floral sources.

Although maltose was reported to occur in some honeys many years ago (Elser, 1924), it remained for van Voorst (1941) and Hurd *et al.* (1944) to show that it is probably a component of all honeys. These findings are supported by the recent analyses of White and Maher (1954b) who found that their 21 test honeys contained an average of 7.11 per cent reducing disaccharides which they classified loosely as maltose.

The L/D ratio of a honey has long been considered a criterion of its crystallizing potential. Since the analyses, from which these ratios were derived, were made without recognition of the presence of reducing disaccharides in honey, the values reported in the literature are suspect. This may help explain the anomalous behaviour of certain honeys which are slow to crystallize even though their ratios are low and of others which crystallize rapidly but have relatively high ratios.

Another method of evaluating the crystallizing potential of honey was suggested by Jackson and Silsbee (1924). They determined the decrease in dextrose solubility in the presence of levulose, of sucrose, and of combinations of the two. By using three-phase equilibria systems and plotting dextrose solubilities at various temperatures they were able to show that sucrose depressed the solubility of dextrose to about the same extent as did levulose. For several characteristic groups of honeys from Browne's data (1908) the three components dextrose, levulose plus sucrose, and water were plotted and "supersaturation coefficients" for the honeys were calculated. While the method may be used to compute supersaturation from the difference between total dextrose and dextrose solubility in the particular honey system, the same criticism as was used previously may be levelled at it, viz., that the maltose content of the honey is not incorporated in the calculations and that the values used for dextrose are probably higher than the true values.

TABLE I — Analyses, by the Adsorption Method, of 49 Honey Samples.\*

Lab. No.	Producing Area	Major	Floral Source(s)** Minor	Total Sugars	Fructose %	Glucose %	Maltose %	Sucrose %	Higher Sugars %
ALBERTA									
A1	Boyle	Sw. Clover		80.79	39.61	32.55	6.82	1.20	0.61
A2	Beaverlodge	Sw. Clover;	Alsike	80.77	38.95	33.68	5.42	1.46	1.26
A3	Lethbridge-Coaldale	Alfalfa;	Sw. Clover	82.96	38.20	32.13	11.15	0.91	0.57
A4	Vauxhall	Sw. Clover		81.53	39.05	31.45	8.71	1.14	1.18
A5	Picardville	Sw. Clover;		80.62	36.90	34.49	7.14	0.65	1.44
A6	Brooks-Rainier	Sw. Clover	Alfalfa	80.50	36.84	31.16	10.84	0.79	0.87
A7	Beaverlodge	Alsike		80.56	39.03	33.40	5.55	0.37	2.21
A8	Lac La Biche	Sw. Clover		80.23	38.32	32.76	6.58	1.55	1.02
A9	Dawson Creek	Alsike		81.10	39.01	33.17	6.68	1.65	0.59
	Average For Alta.			81.01	38.43	32.75	7.65	1.08	1.08
MANITOBA									
M1	Gilbert Plains	Sw. Clover		80.37	39.64	32.09	5.25	2.93	0.47
M2	Poplar Point	Sw. Clover		80.78	38.63	34.22	4.88	1.23	1.82
M3	Libau	Alfalfa;	Sw. Clover	80.86	39.47	34.19	5.51	0.84	0.86
M4	Oakville	Sw. Clover		80.75	39.25	34.77	5.60	0.02	1.11
M5	Terence	Alfalfa;	Sw. Clover	79.82	39.00	33.77	5.68	0.04	1.33
M6	Swan River	Sw. Clover,	Alfalfa	80.86	40.70	34.07	4.78	0.03	1.28
M7	Ethelbert	Alfalfa;	Sw. Clover	80.54	37.72	37.45	4.18	0.05	1.14
M8	MacGregor	Sw. Clover		80.31	39.85	33.98	4.35	0.82	1.31
	Average For Man.			80.53	39.28	34.32	5.03	0.74	1.16
SASKATCHEWAN									
S1	Leacross	Sw. Clover		83.91	39.39	34.71	6.99	1.83	0.89
S2	Manor	Sw. Clover		81.49	40.02	32.61	6.81	1.09	0.96
S3	Porcupine Plains	Sw. Clover;	Alfalfa	81.74	40.36	34.01	5.52	0.65	1.20
S4	Goodsoil	Sw. Clover;	Alfalfa	80.61	39.24	33.43	3.96	2.93	1.05
S5	Prince Albert	Alfalfa;	Sw. Clover	80.38	38.28	33.58	4.85	2.68	0.99
S6	Moose Jaw	Alfalfa;	Sw. Clover	81.40	39.78	34.29	5.11	1.69	0.53
S7	Jordon River	Sw. Clover		80.45	40.74	31.88	5.78	0.57	1.48
S8	Maple Creek	Sw. Clover		80.48	39.18	31.81	6.95	1.42	1.12
S9	Imperial	Sw. Clover		80.71	38.69	33.21	7.20	1.15	0.46
S10	Melfort	Sw. Clover;	Alfalfa	81.41	39.16	33.39	6.32	0.42	2.12

S11	Regina	Sw. Clover	79.87	37.60	32.89	7.18	1.42	0.78
S12	Weyburn	Sw. Clover	79.97	40.37	30.81	6.79	0.04	1.96
S13	Nipawin	Alfalfa;	81.47	37.71	33.79	5.61	2.02	2.34
S14	Yorkton	Sw. Clover;	80.79	39.61	32.55	6.82	1.20	0.61
S15	Tisdale	Sw. Clover;	80.99	38.34	34.52	4.44	1.66	2.03
S16	Regina Plains	Mustard	81.49	36.03	36.73	5.96	1.36	1.41
S17	Buchanan	Sw. Clover	82.08	37.82	33.95	6.21	2.07	2.03
	Average For Sask.		81.13	38.96	33.42	6.03	1.42	1.29
ONTARIO								
O1	Ottawa	Sw. Clover;	82.66	36.76	35.70	4.94	3.39	1.87
O2	Arnprior	Basswood	80.68	35.36	35.47	6.43	0.59	2.83
O3	Anderson	Honeydew	76.82	35.01	27.15	6.77	1.66	6.24
	Average, except honeydew, for Ont.		81.67	36.06	35.58	5.69	1.99	2.35
QUEBEC								
Q1	Chelsea	Basswood	81.78	37.78	33.23	6.82	1.19	2.75
NOVA SCOTIA								
N.S.1	Debert	Goldenrod	82.99	39.17	37.43	5.40	0.09	0.90
N.S.2	Kentville	Goldenrod	83.21	40.31	37.26	4.07	0.41	1.16
	Average for N.S.		83.10	39.74	37.34	4.74	0.25	1.03
	Canadian Average (except honeydew)		81.13	38.77	33.76	6.13	1.17	1.29
FOREIGN SAMPLES								
H1	Norway	Heather	82.51	38.19	37.04	4.07	1.04	2.17
T1	Florida	Tupelo	82.39	44.51	24.93	7.10	2.85	3.00
T2	Florida	Tupelo	80.79	40.95	27.98	6.75	1.47	3.64
T3	Florida	Tupelo	79.59	42.80	26.28	8.04	0.04	2.43
T4	Florida	Tupelo	78.13	41.06	25.68	6.66	1.99	2.74
Or1	Florida	Orange	81.75	38.37	30.41	5.65	4.66	2.66
Am4	U. S. A.	Unknown	81.50	37.35	32.39	6.52	2.75	2.49
Am5	U. S. A.	Unknown	81.01	38.03	27.43	10.28	2.12	3.15
Am6	U. S. A.	Unknown	82.07	37.93	32.92	6.48	2.33	2.41
	Average for foreign samples		81.08	39.91	29.45	6.84	2.14	2.74

\*Analyses re-calculated to 17.5 per cent moisture to facilitate comparison.  
\*\*Identification of floral source by (a) pollen spectrum of sample and/or (b) observation of available flora in producing area.



In the same paper, Jackson & Silsbee (1924) suggested another method of evaluating the crystallizing potential of honey. They evolved a formula to measure "granulation tendency", which is, in effect, the ratio of dextrose minus water to levulose. Shaw *et al.* (1954) used this formula to calculate the granulating tendencies of several characteristic groups of New England honeys.

In this, as in the previously mentioned formulae used to calculate indices of crystallization, no consideration is given to the relatively high reducing disaccharide content of most honeys.

### EXPERIMENTAL METHODS

Selected samples of Canadian honeys were analysed by A.O.A.C. polarimetric, reduction procedures (Austin, 1953-5). The average composition of thirty honeys analysed by this procedure is reported in Table II. It had been intended to use the L/D ratios derived from these analyses to suggest the disposition of honey to the liquid or to the recrystallized pack. In previous work it was suggested (Austin and Jamieson, 1953) that honeys with L/D ratios above 1.14 should be packed as liquid honey. Only eight of the honeys analysed by the above procedures had ratios above this value.

Further samples of the above honeys and of others since collected have been analysed by the selective adsorption method of White and Maher (1954a). The results of these analyses for 40 Canadian and 9 foreign honey samples are reported in Table I.

Briefly, in this method the honey sample is adsorbed on a carbon column and the monosaccharides, disaccharides, and higher sugars are eluted in successive fractions. Fructose is determined in the monosaccharide fraction by copper reduction after the glucose present has been oxidized by hypiodite to glucuronic acid. Glucose, in another sample from the same fraction, is quantitatively oxidized by hypiodite. Reducing disaccharides are determined in the second fraction by copper reduction and the sucrose estimated (in the same fraction) from the increase in reducing power after mild acid hydrolysis. The higher sugars in the third fraction are hydrolysed with strong acid and are calculated as glucose.

On most of the above honeys pollen identification analyses were run in an attempt to establish the flora from which the honeys were derived. However, due to the lack of alfalfa pollen in honeys from areas where this plant is a major source of nectar, the pollen spectra for these honeys are distorted. In such cases additional information on source was supplied by people familiar with the producing area.

In Table II is shown the average composition of 30 honeys analysed by A.O.A.C. procedures and of 40 Canadian honeys analysed by the selective adsorption method. Included also are the results of White and Maher for 19 honeys analysed by the latter method.

### GENERAL DISCUSSION

The establishment of the presence of relatively large amounts of reducing disaccharides (maltose) and the reduction of the indeterminate fractions are the most important features of the selective adsorption method of analysis. In the 40 Canadian honeys analysed these sugars (reducing disaccharides) ranged from 3.7 to 11.15 per cent (mean 6.13 per cent). That they will have an important bearing on honey crystallization is self-evident.

Wykes (1952) has shown that maltose occurs in some nectars but only as a minor component. It is unlikely that it occurs in nectar in sufficient quantities to account for the amounts found in honey by these analyses. On the other hand, there is much evidence to indicate that maltose is formed in the honey stomach of the bee by transglucosidation. White and Maher (1952) have demonstrated the presence of a transglucosidase in honey invertase and that its action on glucose gives rise to maltose and isomaltose. Goldschmidt and Burkert (1955) provide evidence that maltose and isomaltose are present in all honey and are formed in the bee by transglucosidation.

Because of its derivation it is apparent that the maltose content of any honey will depend, to some degree, on methods of apiary management. For example, if a honey is extracted soon after ripening and the enzymes killed by heating it should have a lower maltose content than if it were held without heating for several months. There are other factors which would tend to operate in the same way, viz., rapidity of

ripening, storage temperature, density of the honey, etc. It is not surprising therefore, that honeys derived from the same floral source(s) may differ rather widely in maltose content.

This is borne out by a comparison of certain of the honeys in Table I (e.g.  $A_1$  vs  $A_5$ ;  $M_5$  vs  $M_7$ ;  $S_1$  vs  $S_7$ ;  $O_2$  vs  $Q_1$ , etc.) which were produced in similar climatic areas from approximately the same available floral sources. Inevitably, one must conclude that with a few notable exceptions (such as dandelion, mustard, goldenrod, basswood, etc.) Canadian honeys are derived from mixtures of nectar the relative proportions of which will vary from year to year or, more probably, even from day to day. Hence the floral source of a honey can only be used in a very general way as an index of crystallization and some other method of assessing this potential is required.

TABLE II — Average Composition of Honey as Determined by Different Methods.

Samples	Moisture %	Fructose %	Glucose %	Sucrose %	Maltose %	Dextrins %
33 <sup>a</sup>	17.5	39.44	35.34	2.76	—	—
40 <sup>b</sup>	17.5	38.77	33.76	1.17	6.13	1.29
19 <sup>c</sup>	16.75	38.80	32.20	1.59	7.47	1.24

<sup>a</sup> Polarimetric, reduction methods A.O.A.C. — this laboratory.

<sup>b</sup> Selective adsorption method — this laboratory.

<sup>c</sup> Selective adsorption method — White and Maher (1954b).

Jackson and Silsbee (1924) demonstrated that sucrose depressed dextrose solubility to about the same extent as did levulose. Because of similarity in molecular structure and solubility it is likely that maltose (and other disaccharides) will act in about the same way as sucrose. It is difficult, if not impossible, to evaluate the individual effects of the various disaccharides present on dextrose crystallization in honey so a new criterion of crystallization was sought. Acting on the premise that the "sugars non-dextrose" were similar in their action on dextrose solubility it was postulated that their effects could be lumped or disregarded entirely. The latter assumption was made and a new index of crystallization, the ratio dextrose/water, is suggested.

In Table III these ratios are worked out and compared with the supersaturation coefficients and L/D ratios of Jackson and Silsbee for some of the honeys in Browne's

TABLE III — Comparison of Jackson and Silsbee's Supersaturation Coefficients (Browne's data) with Proposed Dextrose/Water Crystallization Index for the Same Honeys.

Browne's Serial Numbers	Source	Ratio Levulose Dextrose	Supersaturation Coefficient	Ratio Dextrose Water
1 - 8	Alfalfa	1.09	2.86	2.22
27 - 30	Sweet clover	1.08	2.66	2.10
9 - 23	White clover	1.15	2.46	1.98
38 - 45	<i>Compositae</i>	1.22	2.40	1.93
46 - 49	<i>Rosaceae</i>	1.28	2.40	1.93

analyses. From our knowledge of the crystallizing behaviour of certain floral honeys, the supersaturation coefficients appear to be more logical indices of crystallization than the L/D ratios as is evinced from a comparison of the first three items in the table. While the dextrose/water ratios are of a different order of magnitude than the supersaturation coefficients the changes in value for the two series of indices on successive items in the table are truly proportional.

The D/W ratios are much simpler to derive than supersaturation coefficients and can, of course, be calculated from the percentage of only the two components. Aside

from simplicity the D/W ratios fall more logically in line with observed honey behaviour than most crystallization indices. It seems reasonable to postulate that the crystallization potential of a honey is more dependent on the relative amounts of dextrose and water it contains than it is on the proportions of the other components present.

While the other honey components are not used directly in calculating D/W ratios they are, nevertheless, implicit in them. A little thought will show that in order to equate honeys of high and low ratios to the same crystallization tendency, the moisture content of the "high-ratio" honey must be raised at the expense not only of the dextrose it contains but also of each of the other components. It is suggested, therefore, that when honeys are to be compared on the basis of their D/W ratios, their moisture contents should first be adjusted to a common value.

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# Crystallization of Honey. The Effect of Ultrasonic Treatment; the Effect of the Rate of Freezing; and a New Inhibitor of Crystallization for Honey<sup>1</sup>

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## ABSTRACT

*Since honey crystallization is the first step to its deterioration our work on honey preservation began with the study of the various factors effecting crystallization.*

*1) Freezing honey at different temperatures and at various rates showed that above a certain rate of freezing a vitreous condition is obtained which is stable below  $-45^{\circ}$  C. Honey without signs of crystallization frozen at its vitreous state and stored at temperatures below  $-45^{\circ}$  C. for years contained practically no crystals when thawed slowly at room temperature. Further storage at room temperature of the above frozen-thawed honey showed considerable stability to crystallization. Control samples stored at room temperature or frozen at lower rates became sooner or later crystallized depending on the freezing and storage conditions. 2. Treatment of honey by ultrasonics in a magnetostriction oscillator tuned to 9Kcy/sec. for 15-30 minutes destroyed micro-organisms there, eliminated crystals and retarded crystallization for a considerable time depending on the conditions of storage. Also the limpidity of the honey has been considerably improved. 3. A new inhibitor for honey crystallization has been extracted from carob fruits and has been identified as iso-butyric acid. Bees fed with small amounts of the inhibitor produced honey without crystals whereas the control honey produced under identical conditions except the inhibitor had many various sized crystals.*

The crystallization of honey is a process of a very complex and dialectical character. It depends on so many factors acting simultaneously and sometimes in a contradictory fashion, that results of crystallization experiments have to be interpreted with considerable attention. Conclusions may often be erroneous if the results are interpreted only in terms of the isolated factors involved in the experiment. Concentration and state of supersaturation of major components (sugars) as well as of the minor ones (proteins, polysaccharides, etc.), number and size of colloidal particles (the so-called nuclei) and temperature with its varying and contradictory effect upon most of the above elements, are all factors involved in the process. Although we know much about the structure of crystals in general, very little has been learned as yet about the mechanism of initiation of crystallization. Crystallization nuclei are understood to originate from the collisions of molecules coming in contact in certain definite conditions of orientation. When the necessary conditions exist and when a crystal is already present in the solution, crystallization proceeds at once; but if a crystal is not there to initiate the process and to give the direction to the molecules, the latter have first to orient themselves and build up the original nuclei. A brief theoretical discussion of the principles involved, might help to explain better the problem of honey crystallization. Supposing that we start with a true solution, as we may envisage the honey at the beginning of its formation in the stomach of bees or in the cells of the comb, the crystallization procedure will take the following steps: (1) formation of nuclei, (2) appearance of crystals of gradually increasing size, (3) granulation, i.e. separation in a solid form of masses of crystals. The last stage is a dangerous one because it leaves the supernatant liquid more diluted than honey is, and thus permits the growth of yeast there, which otherwise would not normally grow in a liquid as high in osmotic pressure as honey. It appears, therefore, that the stability of a system such as honey

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will depend, (1) upon the velocity of formation of nuclei, and (2) upon the rate of crystal growth. Von Weirmarn's general formula for the velocity of nuclei formation  $W = K \frac{C \cdot L}{L}$ ; where  $W$  = velocity,  $K$  = constant and  $C$  and  $L$  signify respectively concentration and solubility, states actually that the velocity of nuclei formation depends upon  $(C \cdot L)$  which represents the condensation pressure or supersaturation and upon  $L$  the solubility which represent the resistance to condensation. The degree of supersaturation sets therefore a limit to the size of nuclei, because other things being equal the higher degree of supersaturation at the moment of the formation of nuclei the smaller their size will be.

A more theoretical treatment of the formation of nuclei (which can be defined as the least number of molecules required for the emergence of crystal lattice) involves the entropy of activation besides the energy of activation and the temperature. Assuming that the kinetics of crystallization are similar to those of a chemical reaction, the following theoretical formula of Eyring developed for a perfect gas can be used to determine the speed of reaction:  $\text{Rate} = (KT/h) (e^{\Delta S/R}) (e^{-\Delta E/RT})$ , where  $\Delta S$  = entropy of activation,  $\Delta E$  = the energy of activation,  $T$  = absolute temperature and  $R$  = gas constant.  $h$  = Plank Constant.  $k$  = Boltzmann Constant. With the other factors constant the rate of reaction will increase when the entropy of activation increases, the energy of activation decreases and the temperature increases. In crystallization a more ordered state is realized and therefore the entropy of activation is appreciable and is also negative. This makes the reaction rate relatively low and highly dependent upon the entropy of activation. It also explains the reluctance of a supercooled liquid to initiate the deposition of crystals as compared with the readiness with which crystals grow (more entropy of activation is required for the first stage of crystal building).

The systematic study of nucleus formation in undercooled melts and solutions was initiated by Tammann and his co-workers as we are going to see in more detail later on. The important point in Tammann's work is that it has shown that the rate of nucleus formation does not generally increase indefinitely as the temperature is lowered. The theoretical basis for this lies in the fact that an activation energy is associated with crystallization and therefore raising the temperature increases the concentration of activated (reactable) molecules. Thus lowering the temperature favors one factor (the lowering of activation energy) contributory to ready crystallization, but is unfavorable to another (high activation of molecules). Furthermore decreasing temperature increases viscosity which influences crystallization as we know from the extreme case occurring in glasses whereby cooling glass becomes so viscous as to assume a permanently amorphous apparently solid form.

The technique developed by Tammann permits the two factors (nuclei formation and crystal growth) determining the size of crystals to be separated and measured by a nucleus number, which refers to the number of crystallization centers appearing in a definite amount of the melt in a specified time, and a linear crystallization velocity representing the growth rate of the centers in one direction.

Once the nuclei are formed they will grow according to Noyes-Nernst formula for crystal growth:  $V = \frac{\Delta}{l} S(C \cdot L)$ ; where  $V$  = velocity,  $\Delta$  = diffusion coefficient,  $l$  = length of diffusion path and  $S$  = surface area of dispersion phase,  $C$  and  $L$  being concentration and solubility as before.

It becomes obvious from the above formula, how the number and size of the nuclei influence the speed of crystallization by determining the values of  $S$  and  $l$ .

We have said before, that higher supersaturation will result in smaller size nuclei and therefore in great specific surface and greater surface energy per unit of mass. But if the surface energy for small crystals is greater than for larger ones, the larger crystals will grow at the expense of the more soluble smaller crystals; solubility in general increases with the curvature and the curvature becomes greater as the particle size decreases.



The formula shows also that proteins and polysaccharides present in honey will influence crystallization by altering the value of  $\Delta$ . Furthermore, large heavy organic molecules such as proteins, polysaccharides, etc. when attracted by the molecules in solution influence not only the speed of crystallization, but also the form of the crystals by their different attraction on the different faces of the crystals and sometimes have also inhibiting effect on the crystallization in general. (Du Nony, 1926; Pryce-Jones, 1953; Marshall, 1935).

Rise of temperature affects conditions for crystallization in different ways; it alters the degree of supersaturation, increases the speed of molecules and also increases the number of collisions between them and the surface of the nuclei. Not all collisions lead to the formation of nuclei; only between the slowest moving particles collisions might lead to the formation of nuclei. In most cases nuclei formation velocity is diminished by the rise of temperature. If the rate of formation of nuclei is high and that of crystals low, then we might expect the final particles to be small; in the contrary case they will be large. If both velocities are high or both are low, systems will be obtained having many different sized crystals.

Proceeding now to the more concrete experimental data on the effect of temperature upon nuclei and crystal formation obtained by Tammann with melting substances we will have this to say (Tuchschneid, 1936): Tammann showed (Fig. 1) that the number of crystal nuclei formed in the unit of volume and time, near the freezing point, is very small and that with the lowering of temperature it increases rapidly and reaches a maximum. By further lowering of the temperature the number of nuclei formed decreases gradually and finally becomes zero (curve NF of Fig. 1). The curve of the number of crystals formed (CF) follows a similar path. The character of the curve is more or less the same, only the change there begins earlier and also ends earlier in the temperature scale, and the curve also has a lower maximum.

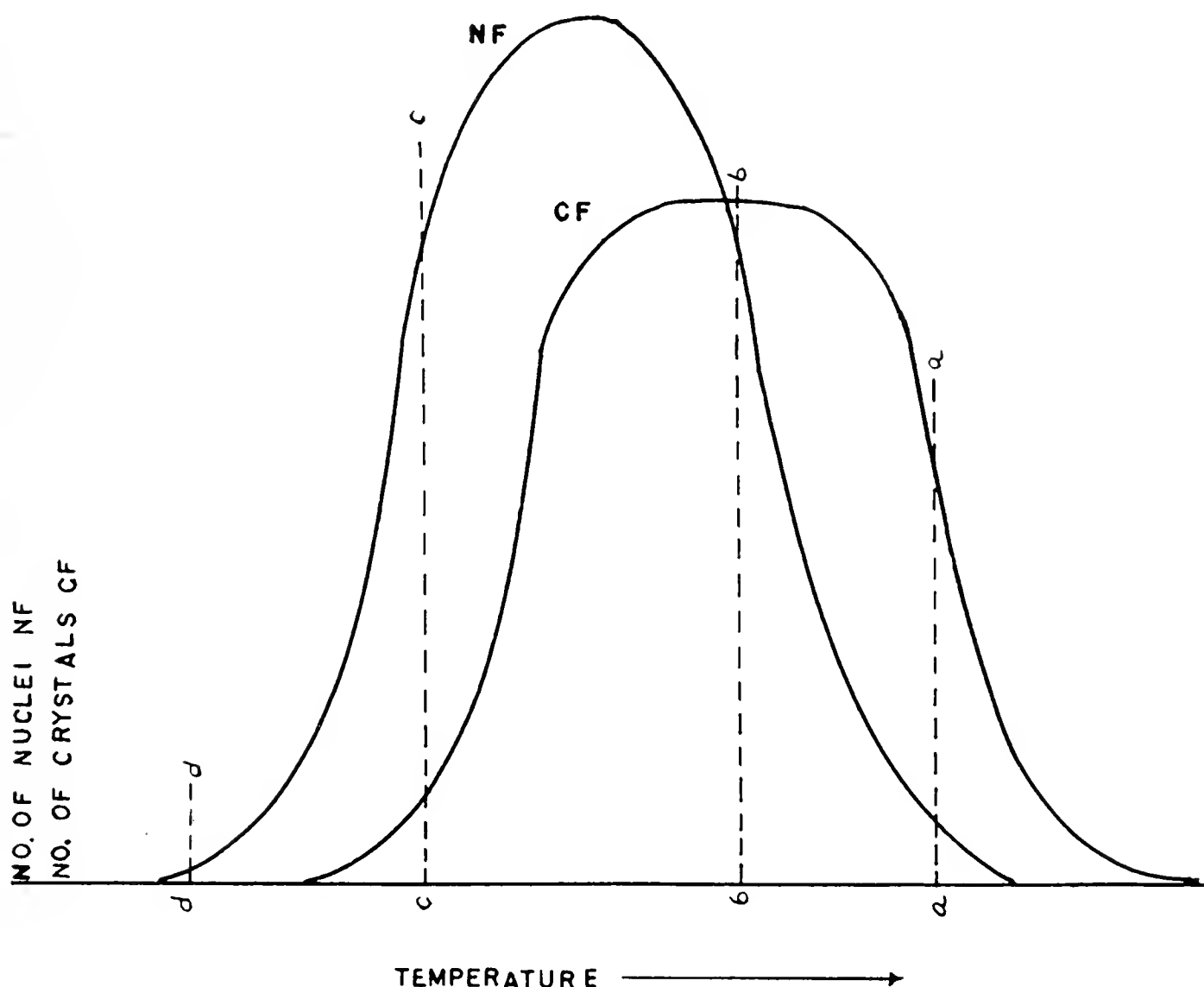


Fig. 1. Curves showing the nuclei (NF) and crystal (CF) formation with temperature changes according to Tammann.

At a point (a-a) a little below the freezing point the number of nuclei is still small but the number of crystals is relatively high. A few large crystals will be formed. At lower temperatures (b-b) both values will be high and therefore we will have many

crystals but of a rather fine structure. At point (c-c) where the number of nuclei is high and the number of crystals small, we will obtain a very fine structure; and at a still lower temperature (d-d) crystallization will not occur at all. The liquid under such conditions will change to an amorphous vitreous state which actually differs only from its previous liquid one by its much higher viscosity. Both liquid and vitreous states are characterized by the disorderly arrangement of molecules, whereas crystalline structure is a very orderly one. We shall come now to our experiments. In view of the above mentioned data of Tammann (Tuchschneid, 1936) and our own experimental results on rapid freezing with many other foods, we decided to organize a freezing experiment of honey but at very high rates of freezing. Starting with a fresh honey, early in the season, which had practically no crystals and probably only a few nuclei, we proceeded by freezing a number of samples at various freezing rates beginning with freezing in air from 0 to  $-78^{\circ}\text{C}$ . and ending by immersion freezing in alcohol-dry-ice baths. In order to produce as many variations in freezing rates as possible we have used glass tubes and vials of different diameters, as containers for honey. When the freezing rate was sufficiently high (immersion freezing or freezing in air at very low temperatures) we could always obtain the vitreous state without signs of crystallization. At lower freezing rates, on the other hand, we had a crystallized structure. When the honey from the vitreous state was brought back to the liquid one, by letting it thaw (melt rather) at room temperature, the liquid contained no crystals. The samples frozen at low rates contained plenty of crystals when thawed under the same conditions. In the vitreous state honey will keep for an indefinite time, without the slightest change, provided that the temperature of storage is low enough to preserve the vitreous state unchanged. We have observed that storage of frozen honey in the vitreous state at temperatures below  $-45^{\circ}\text{C}$ . (in plate freezer) was safe for the preservation of the vitreous state unchanged.

In my opinion freezing honey very rapidly to a vitreous state and then preserving it at low temperatures (below  $-45^{\circ}\text{C}$ .) is the ideal method of preservation for a very long period of time. Every other method, we know, will eventually produce changes in color, aroma, taste and the rheological properties of honey in general. Even if by special treatment, (heat, ultrasonics, inhibitor) the granulation is prevented, other minor changes will occur in time. To see the effect of temperature on the crystallization and the quality of honey in general, we kept samples at all temperatures from  $-45^{\circ}\text{C}$ . to  $+35^{\circ}\text{C}$ . The general conclusion is that at  $-45^{\circ}\text{C}$ . the honey will keep indefinitely, provided that it was frozen to the vitreous state before storage. As the temperature of storage rises from the freezing point up, the granulation is retarded and at about  $+35^{\circ}\text{C}$ . crystallization was practically prevented, at least during the two year period of our experiment. But on the other hand at  $+35^{\circ}\text{C}$ . considerable damage to the quality of honey occurred before the end of the first year of storage. The color was darkened, the aroma was lost and a taste of burned sugar developed. This fact shows that the extensively used heat treatment of honey to prevent crystallization is not totally innocuous to the quality as many people think. Furthermore, with this process as it is actually applied (the heating temperature reaches at the maximum  $150^{\circ}\text{F}$ .) it is rather doubtful if it is effective in destroying the nuclei adsorbed on solid particles, found in honey, and which require higher heat treatment than the usual crystals in order to be eliminated. This is apparently the reason for which heated honey recrystallizes again during the storage forming large crystals.

A good substitute for the ordinary heat treatment which, for a viscous product like honey, presents the danger of overheating in some surfaces and underheating in others, would be dielectric heat. Honey seems ideal material for dielectric heat treatment because it is homogeneous and has a high "loss factor" which ranges from 6 to 8. Preliminary experiments with a Westinghouse 1 Kw radio frequency generator showed that granulated honey could be melted easily and quickly at temperatures as high as  $65^{\circ}\text{C}$ . without the danger of overheating.

The cost of operation would be actually very small since a 15 Kw unit produces 51200 BTU per hour which would be sufficient to heat more than 500 lbs. of honey by  $90^{\circ}\text{F}$ . (sp. heat of honey around 0.66 from extrapolation of sugar sol. 50% which has 0.71). Since the electrical energy used by such a unit is calculated to be \$0.30

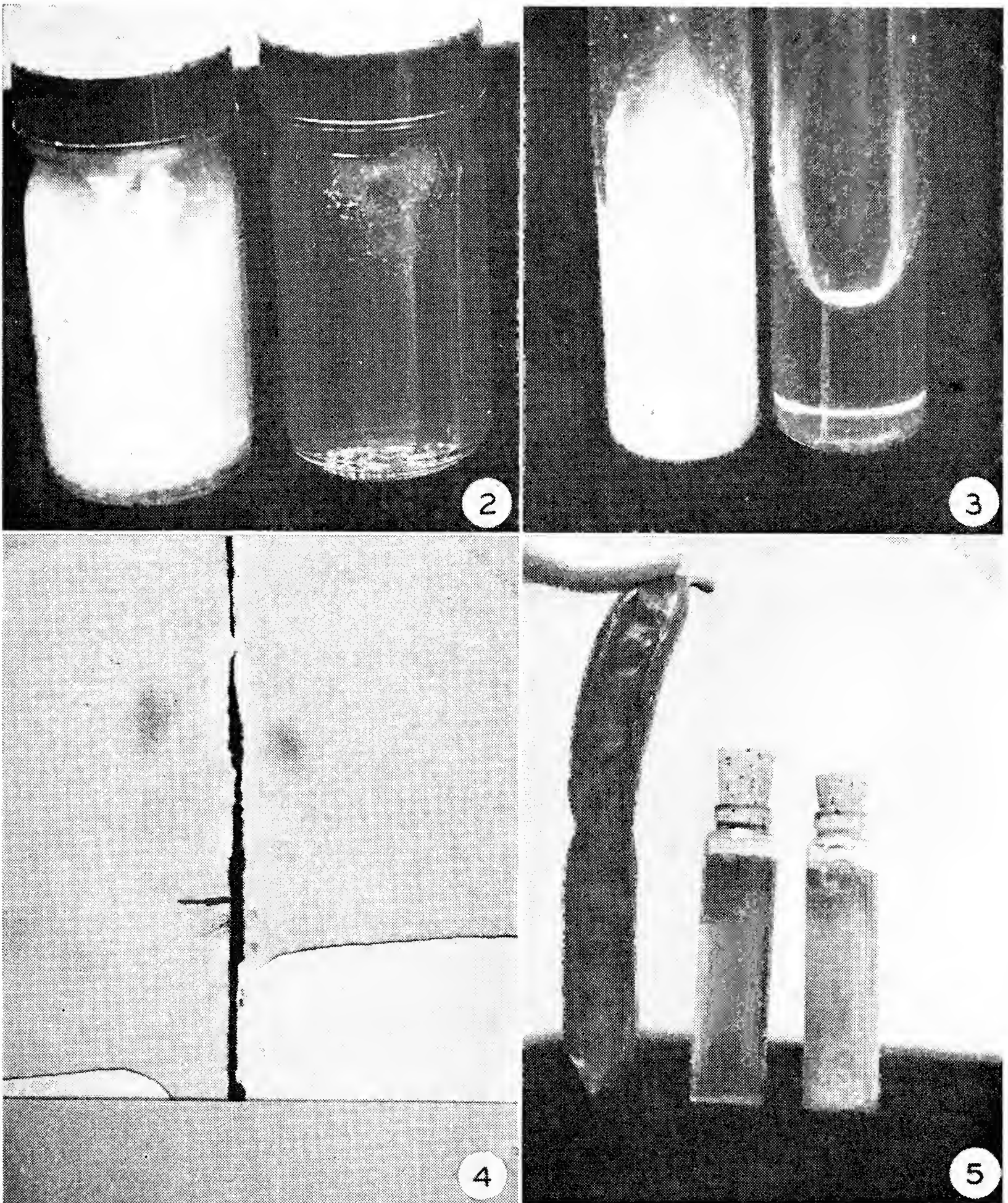


Fig. 2. Showing the effect of dielectric heat on crystallized honey, left granulated honey, right the same honey after treatment with dielectric heat.

Fig. 3. Showing the effect of ultrasonics on crystallized honey, left granulated honey, right the same honey after treatment with ultrasonics.

Fig. 4. Paper chromatograms showing spots produced by carob syrup (right) and by isobutyric acid solution (left).

Fig. 5. Showing the effect of isobutyric acid on honey crystallization, left carob fruit, in the middle honey added with 0.3% isobutyric acid stored for 15 months at 15°C., right control honey under the same conditions of storage.

per hour and the cost of replacing the tubes would be about the same, the operation cost of heating honey would probably be around 1/10 of a cent per pound. The only drawback to the industrial adoption of the process would be at present the initial equipment expenditure which is high (about \$1000 per Kw power). But it is reasonable to expect that with the wide application of dielectric heat in modern industry and in foods particularly (Cable, 1954) soon the cost of such equipment



will decrease considerably, to permit the honey industry to make a profitable use of this new tool of modern technology. According to Scherman (1948) the total cost of all elements of operating cost rarely exceeds the 10 cents per hour per Kw of output. In the case of honey it would amount to about 3.3 cents per pound of honey which is I believe lower than the heating cost by the presently used methods (about 5 cents per pound). Dielectric heat has also another advantage over convection heat in regard to honey. Honey as we mentioned above has a loss factor between 6 and 8 whereas bees wax has only 0.02. This means that when we apply dielectric heat to honey containing wax we can warm the honey without much affecting the temperature of wax and so we can separate them easily. This is very important for thixotropic honeys like heather (*Calluna vulgaris*) honey for which extraction is a major problem (Blair Scott, 1953).

We have not had the time yet to make exact measurements with thermocouples of the limit of the rate of freezing beyond which crystallization will not take place with honey in regular size containers; we expect to do it soon. But we can imagine from the above results that honey placed in small cans can be frozen to its vitreous state by immersion freezing with shaking in alcohol-dry-ice bath ( $-78^{\circ}\text{C.}$ ) or in ether-dry-ice bath ( $-120^{\circ}\text{C.}$ ). For larger containers freezing in liquid nitrogen or similar very rapid freezing techniques will probably be needed.

The second part of our experiment deals with the ultrasonic treatment of honey. We have found previously (Kaloyereas, 1955) that ultrasonic treatment of honey for 15-30 minutes in a magnetostriction oscillator turned to 9 Kcy/sec. not only affected the microorganisms present, but also eliminated the existing crystals and retarded further crystallization for a time depending on the conditions of the subsequent storage. Fig. 3 shows samples of honey subjected to the treatment and stored at  $15^{\circ}\text{C.}$  for 15 months together with untreated samples. This work has already been published in a preliminary form and further experiments in this line would be justified only if we had a higher power instrument for ultrasonic waves production, by which further information on the subject would be obtained. Unfortunately we were unable to secure such instruments and therefore we postponed our further experiment on this line until the appropriate equipment will be available.

We pass now to the third part of our experiments: the study of a new inhibitor of crystallization. During the last world war in Greece, carob syrup was used as a substitute for sugar. The carob tree (*Ceratonia siliqua*) grows in the Mediterranean countries and the fruits when dried contain a large amount of sugar, mostly sucrose (Kaloyereas, 1938). Many unsuccessful attempts were made in the past to produce crystalline sugar from this syrup by the usual process of sugar manufacturing. After long experimentation and the use of special treatments with alcohol Oddo in Italy and Veiss in Greece succeeded in producing crystallized sugar from carobs but both processes proved to be too expensive for industrial application (Kalaidites, 1955). It was suspected that some unknown inhibitor of crystallization existed in carobs which passed into the syrup during the extraction process. When the problem of honey crystallization attracted attention here, two years ago, we thought immediately of the possibility that the unknown factor responsible for the difficulties encountered in the production of sugar from carobs might have in preventing crystallization of honey. First we focussed our attention on the polysaccharides of the carob syrup and after we had extracted them by precipitation with alcohol, we tried these extracts on honey. They did not prevent crystallization.

We worked further with the various fraction of the carob syrup until we located the inhibitor in the low fatty acids fraction. Further research with paper chromatography<sup>2</sup> and the strong smell of the involved substance helped us to identify the substance we were after as iso-butyric acid. This low molecular weight fatty acid has a very strong odor and thus can be easily detected. The next step was to use pure iso-butyric acid in our inhibition of crystallization experiments with honey in order to produce quantitative results. This was done and we have found that a 0.3 per cent iso-butyric acid

<sup>2</sup>The paper chromatography technique applied consists in using n-butanol-ammonia solvent and Bromocresol Green as color developing agent. The carob syrup solution before being put on the paper was made alkaline with ammonia. The R<sub>f</sub> value of the blue spot was 0.13 and the same R<sub>f</sub> value was obtained with the pure iso-butyric acid (Fig. 4).

was a sufficient amount to prevent crystallization in honey for an indefinite period at 15° C. (Fig. 5).

Having thus established the fact that iso-butyric acid added to a certain proportion in the honey was able to prevent crystallization or retard it for an indefinite period of time, we decided to proceed further with feeding studies on bees. If the inhibitor, we thought, was introduced into the honey from the beginning of its formation in the stomach of bees, the chances were that the inhibitory effect would be more pronounced than when it was introduced in honey having crystals and nuclei in considerable amounts, as usually is the case with extracted honey. The task of feeding the bees was undertaken by Dr. Oertel, who has been helpful also in several other ways in this work, by providing honey, literature, etc.

A number of hives were selected early in March for the experiment and to solutions containing 50 per cent sucrose various amounts of iso-butyric acid from 0.25 per cent to 5 per cent were added. It was observed that when 0.25 per cent iso-butyric acid was added the mixture was more attractive to the bees than the pure sucrose solutions; but when 5 per cent iso-butyric acid was added the control sugar solution was taken better by the bees. The strong smell of iso-butyric acid probably made the mixture less attractive in this case. When levulose was used instead of sucrose the amount of iso-butyric acid could be increased to 1.6 per cent and the mixture was still more attractive than the 50 per cent levulose solutions and far more attractive than the 50 per cent sucrose solution. On the 10th of May the first honey was extracted from the experimental hives and examined. The honey produced from the control hives (bees fed only with sugar solutions) showed a considerable number of various sized crystals under the microscope. Honey produced by bees fed with sugar solutions containing iso-butyric acid had no crystals at all, tasted better, and was far more limpid.

For a full evaluation of these results we will have to wait and see how long these samples will keep under storage safe from crystallization. Also it is of interest to us to investigate the mode of action of this inhibitor in preventing crystallization, for the possible implications that the process might have; but the fact remains that a new inhibitor of honey crystallization has been discovered and that this inhibitor is effective not only when added directly to honey but also, and more effectively so, when it is introduced there by the bees.

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# The Composition of Honey

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## ABSTRACT<sup>2</sup>

*A survey is made of the present state of our knowledge of the composition of honey. The picture has become increasingly complex as new information, obtained by new techniques, has become available. The carbohydrates may originate from the plant, be produced during honey ripening, or may appear afterward. Acids may also originate from the plant or be introduced by the bee, directly or indirectly. The enzymes likewise may originate in the plant or bee; further investigation of nearly all categories of materials present is required before a full understanding may be had of the chemistry and biochemistry of honey and its production.*

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<sup>2</sup>Complete manuscript has been published in *Bee World* 38: 57-66. 1957.



# Mineral Nutrition, Nectar Secretion, and the Bee-Flower Relationship

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## ABSTRACT<sup>1</sup>

The extent of seed or fruit yields in cross-pollinated honey plants, and the size of the honey harvest from the flowers of these plants, are functions of the amount of nectar secreted and the number of flowers produced.

The influence of mineral nutrition on nectar secretion and flower production was studied in two species, snapdragon (*Antirrhinum majus*), and red clover (*Trifolium pratense*). Snapdragon was grown at two levels of nitrogen, phosphorus, and potassium, and red clover at three levels of phosphorus and potassium.

Nectar yields in snapdragon were substantially less at the higher level of each element. The nitrogen effect was inversely correlated with the amount of vegetative growth; plants high in nitrogen grew luxuriantly and yielded little nectar. The interrelationships of phosphorus and potassium effects on growth and nectar secretion were not clear-cut.

Mean yield of nectar per red clover floret was highest at the intermediate level of potassium and the low and intermediate levels of phosphorus. High levels of phosphorus and low levels of potassium reduced secretion markedly. Part of the variation in nectar secretion could be accounted for in terms of the regression of nectar yield on inflorescence size.

High levels of potassium consistently reduced nectar concentration in both species. This effect appeared to be independent of potassium-induced variation in nectar volume.

Very high ratios of potassium to phosphorus in the mineral supply resulted in strongly vegetative plants with few flowers. High levels of phosphorus, on the other hand, produced smaller plants which flowered abundantly but whose flowers secreted relatively little nectar.

In the light of these effects on secretion and flower production it was concluded that levels of nitrogen, phosphorus, and potassium which promote moderately vigorous but not excessive vegetative growth and good flowering should produce the best nectar crops.

<sup>1</sup>The complete manuscript has been published in the *Canadian Journal of Plant Science* 37: 220-236. July, 1957.





# Nectar Secretion in Relation to Seed Production in Alfalfa

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## ABSTRACT

Both qualitative and quantitative studies have been made on nectar secretion in alfalfa at Logan, Utah. Studies of qualitative characteristics have been limited primarily to studies of sugar concentration. Small genetic differences in sugar concentration between alfalfa plants have been demonstrated but are considered to have a limited potential for improvement by selection. As sugar concentration at the time of secretion was not determined, there may be more variation between plants at that time. Environmental factors such as relative humidity, soil moisture, and intensity of bee visits have been studied. Under our conditions when nectar accumulates in the flowers, the concentration approaches 80 percent sugar, but it is estimated that it is secreted at about 20 percent. It has been theorized that a measure of sugar concentration, corrected by relative humidity, might be used to estimate intensity of bee visitation.

Consideration was given to the slight increase in sugar concentration that would occur upon inversion of the sucrose. This matter is primarily of academic interest.

Quantitative studies of nectar secretion have been made in more detail. It was found that the volume of nectar per plant rather than per individual flower was the important consideration in attractiveness to both bumble bees and honey bees. A multifactorial hypothesis was postulated as a basis of inheritance. The possibility of improving the nectar secretion of alfalfa by breeding is considered good.

Environmental as well as genetic differences have a strong influence on nectar secretion. Plant density has been studied in some detail. Plants spaced in 48-inch hills or thinned to 12-inch hills in 24-inch rows produced about twice as much seed, nectar per flower, honey bee visits, and pod set as a hay stand.

Because the value of nectar production to alfalfa seed production has been somewhat controversial, it may be well to review the situation briefly. Most students of the problem have concluded that alfalfa is cross-pollinated to a high degree and that bees are essential in pollination. No doubt all workers will agree on the importance of pollen-collecting bees whether wild or domesticated, but the opinions regarding the importance of nectar-collecting honey bees are not nearly so unanimous. For this reason it may be well to consider some of the data concerned with this feature.

In general, men working on the problem in more or less arid conditions (Grandfield 1950, Jones 1950, Vansell 1951, Ostacenko-Kudrjavceva 1941) have found that nectar-collecting honey bees are responsible for an appreciable amount of the seed set. Workers from other regions (Hixson & Graumann 1947, Hobbs & Lilly 1955) have sometimes found just the opposite and some insist that automatic tripping and self-pollination are important (Lesins 1950, Ufer 1932, 1933).

Results obtained at Logan have consistently shown a positive relationship between nectar production, nectar-collecting honey bees, and alfalfa seed yield (Pedersen 1953, 1953). For example, a positive correlation coefficient of  $+0.566^*$  was obtained between nectar sugar per plant and honey bees per plant and values of  $+0.634^{**}$  and  $+0.779^{**}$  for nectar-collecting honey bees per plant and seed yield. It is possible that part of the unaccounted for variation may be caused by differences in sugar composition of the nectar of the different plants (Wykes 1952), but such tests have not been carried out. In addition, nectar production per plant was also found to be associated with attractiveness to pollen-collecting bumble bees (Pedersen 1953). This is considered to be a cause and effect relationship although the physiological significance of nectar production other than to attract pollinators is not known. In other words, the correlations must mean that a high nectar-producing plant has sufficient inherent vigor to produce a large amount of seed as well as the ability to attract pollinators.

<sup>1</sup>In cooperation with Entomology Research Branch and the Utah Agricultural Experiment Station.

Confining and excluding honey bees to alfalfa by means of large 11.5' x 21.5' x 6' plastic screen cages in 1948 and 1949 have shown that without bees practically no seed is produced, while additional pollination by caged bees can increase seed yields from 53 to 62 percent at Logan, Utah (Pedersen and McAllister 1955). Ostacenko-Kudrjavceva (1941) concluded that a good seed "set" was associated with copious nectar secretion and indicated that every possible means of encouraging the flow of nectar should be used.

The low tripping rate of nectar collectors is sometimes given as evidence of their unimportance. However, Bohart *et al.* (1955) indicate that a yield of 350 pounds of seed per acre could be pollinated by nectar collectors in 3 weeks if the fields were in an attractive condition, and Jones (1950) stated that 1500 pounds of seed per acre could be set by nectar collectors in California over a two-month period. It seems safe to conclude that nectar-collecting honey bees are important in alfalfa seed production in the more arid parts of the United States and for this reason continued research in this area is justified.

### QUALITATIVE GENETIC

Various workers (Vansell 1942, Beutler 1940, Boetius 1948, Hammer 1949) have demonstrated that there are differences between genera, species, and varieties in the concentration of the nectar; also that within certain limits bees prefer more concentrated solutions (Butler 1945, von Frisch 1950, Vansell 1942). The range in sugar concentration of the various alfalfa clones with which I have been working is very small, but nevertheless statistically significant. It is believed that the range in concentration at the time of secretion may be considerably greater, but no way of measuring the concentration at this time has been devised. Because of the limited range and the very pronounced effect of the environment on the sugar percentage it is believed that selections based on sugar concentration will be of limited value. Shuel (1952) working with red clover came to similar conclusions.

### RELATIVE HUMIDITY AND SOIL MOISTURE

It is generally agreed that nectar sugar concentration and relative humidity are correlated (Vansell 1934, Scullen 1942, 1942, Park 1929, Beutler 1930, Fahn 1949, Hammer 1949, Oertel 1946, 1944). In a rather limited trial at Logan, Utah, a correlation of  $-0.910^{**}$  was obtained. Under certain conditions this relation is not so clear cut. Factors which may modify this relation include irrigation, fertilization, species, and intensity of bee visitation. After a furrow irrigation at Logan the sugar concentration of the nectar was reduced. In this case it appeared that the increase in atmospheric humidity associated with irrigation rather than the increase in soil moisture was responsible. Somewhat similar results were obtained by Beutler (1930) and Czarnowski (1953). Vansell (1941) concluded that low soil moisture as well as low relative humidity cause an increase in sugar concentration of the nectar and this conclusion is supported by Shuel and Shivas (1953).

### SPEED OF REMOVAL BY BEES

As alfalfa nectar is supposed to be secreted at a concentration of about 20 percent or less and is increased by evaporation, the relative humidity and time of exposure will determine the concentration at any given time. Therefore, a high concentration of nectar should result from slow removal from the flowers as contrasted with a low concentration with fast removal if the humidity is constant.

As indicated in Table I variations in nectar sugar concentration might be useful in comparing the attractiveness or concentration of honey bees on a crop in different localities. For example, if under standardized conditions, the relative humidity were 50 percent, the sugar concentration 25 percent, a high attractiveness or high bee population would be indicated. Whereas, if the sugar concentration were 50 percent the opposite would be true. This, however, is contrary to an interpretation made by Stapel and Lund (1945). They assumed that plants secreted nectar at a lower concentration after pollination than before. Bagged plants, of course, would not be pollinated. Wykes (1951) found that the sugar concentration was lower if frequently

removed which would support the stated theory. Supporting work was also reported by Vansell (1942) and Boetius (1948).

TABLE I — Sugar Concentration of Alfalfa Nectar as Affected by Relative Humidity and Concentration of Honeybees (estimated).

Stands of bees per acre	Relative Humidity						
	20	30	40	50	60	70	80
	Percent of Sugar						
0	80	70	60	50	40	30	20
1	72	63	54	45	36	27	18
2	64	56	48	40	32	24	16
3	56	49	42	35	28	21	14
4	48	42	36	30	24	18	12
5	40	35	30	25	20	15	10

INVERSION

Another factor which might modify the sugar concentration to a limited extent is the rate of sugar inversion which takes place after the nectar is secreted. If one assumes that alfalfa nectar is secreted generally as sucrose and that inversion can occur in the flower, then an increase in sugar concentration would occur in connection with the inversion if the process is normal. This comes about because water is used up in the reaction. If complete inversion occurs the maximum change that could occur is only about 4 percent, consequently this feature is of no great practical importance unless the hygroscopic nature of the sugar solution or its attractiveness is changed by the inversion.

QUANTITATIVE  
GENETIC

While sugar concentration of nectar has only limited value in a breeding program, nectar volume is another story. A threefold range in nectar sugar production was found in a group of alfalfa plants. Furthermore, a heritability of more than 60 percent was indicated. Quantitative inheritance was suggested on the basis of normal frequency distributions obtained in hybrids of high and low nectar-producing parents.

In general, a high production is associated with large flowers and consequently a relatively large amount of secretive tissue (Fahn 1949, Vansell 1941, Andreev 1928). This would appear to be true also when comparing diploid and tetraploid plants (Maurizio 1954).

SUNSHINE

There is general agreement on the necessity of sunshine for nectar secretion. This was remarkably demonstrated by a coincidental sampling in 1950. When sampling followed a cloudy period there was a daily increase in secretion. On the other hand, there was only a minimum daily fluctuation when the sampling period was preceded by fair weather (Pedersen 1953).

SOIL MOISTURE

Although there may not be complete agreement, it is generally thought that fluctuations in soil moisture far from the optimum for growth are not good for nectar secretion (Shuel and Pedersen 1952, Beutler 1930, Fahn 1949, Kenoyer 1916, MacLachlan 1941, Czarnowski 1953). Obviously, a plant in a state of drought is limited in amount of flowering and available water for secretion. On the other hand, excessive moisture can be just as harmful. It is believed that for the best nectar production in alfalfa that the moisture should be ample to provide a vigorous growth, but sufficiently restricted during flowering and seed formation that the plant is in a reproductive rather than vegetative phase. Although data are incomplete, an empirical estimate of four atmospheres (Bouyoucos block method) has been made as the desirable level as an integrated value for the entire season for seed production of alfalfa (Legume

Seed Research Laboratory unpublished). Whether or not a similar value would apply to nectar secretion has not been determined.

Nectar production on field plots was increased from 0.37 mg. per flower to 0.46 by irrigation in 1949 (Pedersen 1953). Percentagewise this is a sizable increase.

#### POLLINATION LEVEL

Nectar secretion on bagged flowers was similar whether bees were excluded, confined, or not molested in a test conducted in 1948. Boetius (1948) and Raw (1953) found that secretion was stimulated by repeated removal while Beutler (1929) could see no difference than if it was removed only once.<sup>1</sup> Teleological significance has been attached to this feature, however, teleology in this field has not been studied recently to any extent.

#### INSECT CONTROL

Applying insecticides for lygus bug control did not affect the nectar secretion per flower in an experiment conducted in 1948 (Pedersen 1953). Total secretion would be increased, however, because the bud blasting caused by the lygus bugs would be reduced by the insecticide application.

#### FERTILIZERS

In an experiment conducted in 1949 nectar secretion was not influenced by the application of nitrogen, phosphorous, manganese, copper, boron, or zinc (Pedersen 1953). The test area was, however, quite fertile. Schontag (1952) found no influence of nitrogen, phosphorus, and potassium fertilizers on nectar secretion of raspberry, two gooseberries, currant, rape, and alfalfa. However, the total secretion of sugar was more because of better flowering on the fertilized plants. Hasler and Maurizio (1950) found that a potassium deficiency resulted in a reduction in the average amount and sugar concentration of nectar secreted in rape, but that lack of nitrogen, boron, magnesium or phosphorous was found to have no marked effect on nectar content per flower. However, they also found total secretion to be favored by adequate amounts of nitrogen, phosphorus, and potassium. Fertilization with boron, manganese or zinc increased nectar secretion per flower and seed yield per acre in sunflower, buckwheat, alfalfa, and sainfoin (Lesik 1953). Shuel (1955) explained results with snapdragon and alsike in favor of a low nitrogen supply for high secretion per flower. He reasoned that with low nitrogen a nitrogen deficit would limit growth thereby causing a surplus of carbohydrates to accumulate. Nectar should then be secreted in abundance. With high nitrogen the carbohydrates would be used in growth and would not be available for nectar secretion. Ryle (1954) concluded that nectar secretion would be poor if growth were limited by potash, but that a surplus of potash would promote nectar secretion if growth were limited by nitrogen or phosphorus.

#### SPACED PLANTS

Spaced plants in 48-inch hills were compared with plants in dense hay stands in 1954. Nectar production on an individual flower basis was favored on spaced plants by about 2 to 1. On the hill planting 0.21 microliters of nectar sugar was obtained per flower whereas only 0.10 was obtained on the solid stand (Pedersen 1955). There was very little variation of production in the spaced planting from July 27 to August 21. However, in the solid stand production started low, increased until August 14, from which time it dropped rapidly. On August 14 nectar production from the two types of stands was not significantly different.

When alfalfa is grown in hills, the plants are larger, have longer, coarser stems, and produce flowers that are slightly larger than when grown in dense stands. The length of the standard petal was determined in a series of measurements to compare flower size. The average length of the standard petals from plants grown in hills was 8.08 mm. compared with 6.68 from the hay stand. This difference in flower size is no doubt reflected in the amount of nectary tissue and as others have found (Andreev 1928, Vansell 1941, Fahn 1949) may account for part of the difference in secretion. It is also very likely that better photosynthetic activity takes place in the open stands.

<sup>1</sup>Pedersen, M. W., C. W. LeFevre, and H. H. Wiebe. 1958. Absorption of C<sup>14</sup> labeled sucrose by alfalfa nectaries. *Science* 127: 758-759.



The higher soil temperature in the thin stand would also favor nectar secretion (Shue and Shivas 1953).

#### THINNED STANDS

Both nectar secretion and seed production were stimulated by thinning. Eight-inch rows were thinned to 24-inch rows with plants in 12-inch hills. This treatment was applied in the fall of 1953 and 1954 to stands established in 1952. Nectar secretion was not checked in 1954, but in 1955 nectar secretion on the plots thinned in 1954 averaged 0.21 ul per flower compared to 0.16 on the plots thinned in 1953 and 0.11 on the plots that were not thinned. Flowering commenced about 10 days earlier on the thinned stands and also the peak in nectar secretion occurred a little earlier than on the hay stands.

Seed yields in 1954 from second crop seed were increased more than 4½ fold by thinning in the fall of 1953 (Table II). The next year when first crop seed was harvested the yields were approximately doubled by thinning. As yields in 1955 from stands thinned in 1953 and 1954 were about the same, it would appear that the stimulation obtained by thinning lasts for two seasons.

TABLE II — Alfalfa Seed Yield as Affected by Thinning an Established Stand.

Treatment	Seed Yield in Pounds Per Acre	
	1954	1955
1. Thinned in 1953	307	422
2. Thinned in 1954	—	427
3. Rows (24" planted at rate of 1 pound per acre)	151	338
4. Hay stand (8" rows planted at rate of 12 pounds per acre)	66	183

An explanation for the stimulation to nectar and seed production derived from thinning is not readily available. No doubt opening up the stand to permit more sunlight to enter per unit of vegetation would be a factor. However, this would not explain the stimulation entirely as equivalent non-thinned stands are not equal in performance. What part the rotting of roots from the plants which were removed would play is not evident. Modification of the carbon/nitrogen ratio, change in the carbon dioxide content of the atmosphere and/or root pruning offer leads for studying the cause of the stimulation derived from thinning.

The proportionate growth and storage rate in roots could be modified by thinning and as storage in roots and seeds occur at the same time this is another feature that could be involved in nectar secretion of a perennial such as alfalfa.<sup>2</sup>

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<sup>2</sup>Pedersen, M. W. 1957. Effects of thinning an established stand, of nitrogen supply, and of temperature on nectar secretion in alfalfa. *Bot. Gaz.* 119:119-122.



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# Nouvelles recherches sur la sécrétion nectarifère de plantes cultivées polyploïdes: *Nicotiana*

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Faisant suite aux recherches sur la sécrétion nectarifère chez les plantes cultivées polyploïdes (Maurizio 1954a, b), on a examiné la quantité, la teneur en sucres et la composition chimique du nectar des formes di-et-tétraploïdes de deux Tabacs (*Nicotiana silvatica* et *N. trigonophylla*).<sup>1</sup> Le nectar fut prélevé au moyen de tubes capillaires en verre, dans les fleurs protégées depuis 24 heures par des bonnettes de gaze; la quantité de nectar fut déterminée par pesée, sa teneur en sucre calculée au moyen d'un réfractomètre Abbé-Zeiss. Les expériences furent renouvelées chacune 5 à 6 fois. La mise en évidence et la détermination quantitative des différentes sortes de sucres fut réalisée par chromatographie sur papier en séries parallèles, par élution et reprise directe au leucomètre (Flood et al. 1947, Nelson 1944, Partridge & Westall 1948, Somogyi 1945, Sulser 1954). Les recherches donnèrent les résultats suivants:

1. En accord avec nos recherches précédentes (Maurizio 1954a, b) les formes tétraploïdes des deux espèces de *Nicotiana* secrètent respectivement 1,5 et 2,6 fois plus de nectar par fleur et par 24 heures que les diploïdes correspondants.

2. La concentration en sucres du nectar chez *Nicotiana trigonophylla* est sensiblement la même pour les formes di-et-tétraploïdes; chez *Nicotiana silvatica* le nectar de la forme tétraploïde a une teneur en sucres nettement plus basse.

3. La quantité de sucres produite par fleur et par 24 heures est, chez les formes tétraploïdes de chacune des espèces de *Nicotiana*, respectivement 1,6 et 2,2 fois plus élevée que chez les diploïdes correspondants.

4. Le nectar frais des deux *Nicotiana* ne contient que trois sucres: fructose, glucose, saccharose.

5. Les deux *Nicotiana* se comportent différemment en ce qui concerne les proportions relatives des trois sucres principaux. Tandis que chez *Nicotiana trigonophylla* le rapport entre saccharose et sucre interverti présente approximativement les mêmes valeurs chez les deux formes (saccharose: fructose + glucose = 0,44 chez 2n et 0,49 chez 4n), le nectar de *Nicotiana silvatica* présente chez la forme diploïde sensiblement plus de saccharose que chez la forme tétraploïde (saccharose: fructose + glucose = 1,95 chez 2n et 0,45 chez 4n). De toute évidence l'hydrolyse du saccharose se produit sensiblement plus rapidement dans le nectar de la forme tétraploïde, tandis que chez *Nicotiana trigonophylla* il n'existe que peu de différence sous ce rapport entre la forme 2n et la forme 4n.

6. Les différences de proportion du saccharose au sucre interverti confirment les observations faites précédemment sur d'autres plantes (Maurizio 1954a, b), selon lesquelles le nectar des plantes diploïdes et polyploïdes contient des invertases d'activité différente.

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<sup>1</sup>Les semences de *Nicotiana* ont été aimablement mises à ma disposition par l'Institut des Tabacs de la S.E.I.T.A., à Bergerac (France), que je tiens à remercier ici.



# Nectar Yields of Various Plant Species at Baton Rouge in 1955

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## ABSTRACT

Nectar was obtained in appreciable quantities from the blossoms of a number of plant species through the use of a centrifuge and capillary tubes. Several samples of blossoms from holly, wild grape, and smartweed did not yield any nectar. Results obtained during the past few years indicate that nectar can be easily obtained from a number of species; providing enough material for chemical analyses.

The difficulty of getting adequate samples is probably the reason why the sugar composition of nectar from different species of plants has not been more thoroughly studied. Swanson and Shuel (1950) have shown that by the use of a centrifuge and calibrated centrifuge tubes nectar can be readily obtained from red clover (*Trifolium pratense*). Bailey *et al.* (1954) used a similar method to get nectar from white clover (*Trifolium repens*), Satsuma orange (*Citrus nobilis unshiu*), and alfalfa (*Medicago sativa*). In 1955 a centrifuge was used to determine the amount of nectar obtained from various species of honey plants at Baton Rouge, La.

Mature or nearly mature blossoms were taken for testing. None were taken during unfavorable weather — in rain or at times of strong winds or high humidity. Clover blossoms were protected from large nectar-collecting insects by screen cages. All other blossoms, except vetch, were covered with cheesecloth bags for 6 to 72 hours before sampling.

The racemes of vetch and sweetclover had averages of 15 and 18 open florets, respectively. The heads of red clover, white clover in a pasture, and white clover in a greenhouse had 104, 35, and 47 florets, respectively. The outer portions of the florets of red clover, white clover, and vetch and the petals of basswood and broccoli were removed so that the nectar-secreting parts could be placed in Bauer and Schenk calibrated centrifuge tubes. Blossoms were centrifuged at 1500 r.p.m. for 5 minutes. The volume of nectar was read directly in the tubes. When the amount available was sufficient, nectar was removed with a micropipette and the percentage of total solids determined by the use of an Abbé refractometer.

The amount and concentration of nectar from blossoms of seven plant species are given in Table I. Blossoms of holly (*Ilex opaca*), wild grape (*Vitis* sp.), and smartweed (*Persicaria* sp.) were centrifuged, but no nectar was obtained. Honey bees were visiting holly and grape blossoms near the covered sample flowers, but none were seen on smartweed blossoms. Perhaps larger samples would have contained some blossoms from which nectar could have been obtained, since some blossoms of other species did not yield nectar. Of the species given in the table, basswood probably produces the greatest amount of nectar in a short time. A fairly large tree with an abundance of blooms may yield from 1 to 6 quarts in a day. Red clover heads yielded more nectar than white clover that was growing in a pasture. However, the latter had many more blossoms per acre, bloomed over a longer period, and was preferred by honey bees, and so is a much more valuable honey plant in the Baton Rouge area. Vetch contained a fairly large amount of nectar per raceme, but it is seldom visited by honey bees in this area. It is a honey plant in northern Louisiana, Arkansas, and other States.

A comparison of results reported in recent years for the production of red and white clover nectar is difficult, largely because in some cases yields are given by weight of nectar, in others by volume, or by sugar as reported by Ryle (1954). It is not always clear whether the "head" or the "floret" is meant, as in red clover, or the "raceme" as in vetch, or the individual flower, as in basswood. In red or white clover, where the head or inflorescence is composed of many florets, the amount of nectar

<sup>1</sup>In cooperation with Louisiana State University.

TABLE I — Nectar Yields of Various Plant Species at Baton Rouge, La., 1955.

Plant species	Total heads, flowers, or racemes	Nectar yield per flower or raceme		Average sugar content
		Average	Range	
	Number	Microliters	Microliters	Percent
Basswood ( <i>Tilia</i> sp.)	680	1.64	0 to 6	43
Broccoli ( <i>Brassica</i> sp.)	186	1.12	0 to 2	42.7
Eardrop vine ( <i>Brunnichia</i> sp.)	300	0.33	0 to 0.8	60
Hubam sweetclover ( <i>Melilotus</i> sp.)	304	0.37	0 to 2	38
Red clover ( <i>Trifolium pratense</i> )	171	4.8	0 to 27	36.7
Vetch ( <i>Vicia</i> sp.)	209	1.2	0 to 13	44.6
White clover ( <i>Trifolium repens</i> ), Pasture	80	3.2	1 to 12	55.4
Greenhouse	102	11.0	1 to 36	56

obtained will vary according to the number of open florets that contain nectar. For any particular species the centrifuge method of nectar extraction will probably give more consistent results than the use of a pipette or examination of the contents of the bees' honey stomachs.

YIELDS FROM RED CLOVER

Boëtius (1948), in Denmark, collected nectar from field-grown red clover by means of a pipette. He found that the nectar yield ranged from 0.41 to 0.90 mg. per flower, and the sugar concentration from 17.4 to 53.2 percent, with most samples between 33.6 and 36.1 percent. In similar collections Maurizio (1954), in Switzerland, found that the polyploid flowers yielded about 0.281 mg. in 24 hours, and that the average sugar concentration was 23.4 percent. Swanson and Shuel (1950), in Ohio, collecting nectar by means of a centrifuge, found the average yield from red clover flowers grown in a greenhouse to be 9.4 microliters per 100 florets. Shuel (1952) reported yields of 15.1 to 18.3 microliters per gram of inflorescence for red clover in a greenhouse, and sugar concentrations from 66.5 to 69.5 percent.

A study of the relation of volume to weight of red clover nectar at Baton Rouge showed that 1 microliter weighed 1.3 mg. when the average sugar concentration was 28 percent. On this basis the yield of nectar from red clover heads reported in Table I is fairly close to that given by other workers. Since the sugar concentration of nectar depends largely upon the amount of moisture in the air (Oertel, 1944), we can expect considerable variation, depending upon time of day and climatic conditions. Probably the seemingly high sugar concentration reported by Shuel (1952) was caused by conditions within the greenhouse.

Hammer (1949), in Denmark, removed the contents of the honey stomachs of bees caught on red clover flowers and found that the sugar concentration in 1948 ranged from 41-52 percent in the forenoon to 45-48 percent in the afternoon, in other years from 17.1 to 57.1 percent. The figures given by Hammer probably are **not as** representative as those obtained from nectar taken directly from the florets. Oertel *et al.* (1951) have shown that the longer sucrose sirup is in the bees' stomach the greater is its dilution. It is likely that the same is true for nectar.

YIELDS FROM WHITE CLOVER

The amount of nectar produced by white clover has not received the attention given to nectar from red clover, in spite of the former's importance as a honey plant. Boëtius (1948) reported that nectar production ranged from 0.19 to 0.28 mg. per flower, with a sugar concentration from 39.9 to 51.7 percent. Maurizio (1954) reported



an average yield of 0.088 mg. in 24 hours for the polyploid form with an average sugar concentration of 30 percent. In a limited study at Baton Rouge 1 microliter of white clover nectar weighed 1.04 mg. On this basis the yields reported by Boëtius are much larger than those reported in Table I (for a more detailed discussion see Oertel 1956), while those reported by Maurizio are nearly the same. Beutler (1953) has suggested that standard methods of investigation be used for a species that occurs in many areas. The method of nectar removal and its measurement (volume or weight), time of day, age of blossoms used, and period of protection (if any) from insects could be standardized. Important variables such as temperature, humidity, solar radiation (Shuel 1952), soil, and the variety of the species studied are not likely to be controlled, especially for plants growing in the field. Plants growing in the greenhouse may yield more nectar than outdoor plants. White clover and white sweetclover flowers grown in the greenhouse at Baton Rouge have consistently yielded more nectar of a higher sugar concentration than flowers growing out of doors. It is not known whether conditions in the greenhouse were more favorable or caging of outdoor plants reduced the nectar yields. The mineral and fertility components of the soil may affect nectar yields. Results recently reported by Ryle (1954) and Shuel (1955) and earlier by Stapel and Götzsche (1941) show that the application of fertilizers may or may not affect nectar yields, depending upon the species and the fertility of the soil before the experimental treatments were made.

### SUMMARY

The centrifuge method of obtaining nectar from red clover as developed by Swanson and Shuel has been used in similar studies on basswood, broccoli, eardrop vine, Hubam sweetclover, red clover, vetch, and white clover at Baton Rouge, La. The nectar yields and sugar concentration for red clover were fairly close to those reported by other workers. Yields of white clover nectar were considerably lower than those reported by Boëtius in Denmark. The ratio of volume to weight was 1 to 1.3 for red clover and 1 to 1.04 for white clover nectar. White clover and white sweetclover plants in the greenhouse produced more nectar of a higher sugar concentration than field-grown plants. In order that comparative figures can be obtained in widely separated areas, standardized methods of investigation are needed. The centrifuge method appears to provide sufficient nectar for a study of the sugars present in the nectar of many species of plants.

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# Rearing Honeybee Larvae in the Laboratory<sup>1</sup>

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## ABSTRACT

Royal jelly was taken from queen cells of the honeybee and fed directly to worker larvae in the laboratory. The adults that developed on it were queen-like in all characteristics. Royal jelly that was stored at 5°C for about a year and then fed to larvae produced 2 adults that were rather queen-like, but many other adults that were worker-like in all characteristics, or were queen-like in only one or two characteristics. Preliminary experiments on the fraction of royal jelly that contains the substance responsible for differentiation of castes are reported. The significance of the results are discussed briefly.

Conclusive experiments on dimorphism in the female honeybee (*Apis mellifera* L.) are difficult to perform if the larvae must be reared by colonies of bees. The lack of strict experimental control over the environment in the hive often renders the proper interpretation of results impossible. Techniques must be devised for rearing honeybee larvae in the laboratory if the causes of dimorphism are to be determined.

Rhein (1933) reared honeybee larvae on royal jelly in the laboratory and found that only workers developed. According to Butler (1955) the experiment has been repeated by others with the same results. In a preliminary report (Weaver, 1955) it was stated that queens could be reared in the laboratory on royal jelly. The present paper presents the data upon which this conclusion was based, and new experiments on rearing honeybee larvae in the laboratory.

In order to produce royal jelly, larvae less than a day old were grafted into dry wax queen cell cups, and reared in colonies by the methods given by Weaver (1957). If fresh royal jelly was needed for an experiment the jelly immediately surrounding the larvae was pipetted from the cells. If the royal jelly was to be stored for use at a later date, all jelly was removed from the cells daily; the larvae were then returned to the same empty cells and were fed by the colony until the jelly was removed on the following day. The larvae reared in the laboratory were taken from worker cells when they were about one and a half days old and were reared in a constant temperature cabinet at  $34 \pm 1^\circ\text{C}$  and about 75 per cent relative humidity. Mature adults were dissected, and several measurements were made on them by essentially the same methods as were described in detail by Weaver (1957). Adults reared in earlier experiments were dissected without being fixed, and several measurements of the extent of dimorphic development were added as the study progressed.

Table I gives the measurements of some of the bees reared during these experiments, and the means and ranges of the measurements of the 42 normal queens and 173 normal workers reported by Weaver (1957). The basitarsal index shown in Table I is the length of the proximal segment of the metathoracic tarsus divided by its breadth; the remainder of the measurements are self explanatory.

## FRESH ROYAL JELLY

In the first series of experiments queen larvae about 36 hours old were removed from their cells and replaced immediately by larvae of about the same age taken from worker cells. A screen lined with dampened cotton excluded adults from further contact with the experimental cells. Every 2 hours the larvae were transferred to fresh queen cells from which larvae of approximately their own age had just been removed. When a larva was mature, the cell was closed by affixing the distal end of a queen cell that had contained a pupa. About 2 days before the adult was expected to emerge, the cell was moved to an emergence cage in a constant temperature cabinet.

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TABLE I. Measurements of some Bees Reared on Royal Jelly and Extracts of Royal Jelly in the Laboratory.

Treat. No.	Bee No.	Weight cg.	Basitarsal		Abdomen mm.		Diameter Ovary mm.		No. Ovarioles		Sperm. Diam. mm.	Tongue Length mm.	Mand. Gland. Length mm.	No. Barbs on Sting
			Length mm.	Index	Breadth	Length	Right	Left	Right	Left				
1	1	—	2.7	2.2	4.3	8.4	1.6	1.7	109	121	—	1.5	1.8	4
	2	—	2.3	2.1	4.6	7.6	1.3	—	116	—	—	1.9	1.9	—
2	3	—	2.6	2.4	4.9	10.1	1.9	1.7	161	133	0.9	1.7	1.9	3
	4a	—	2.6	2.1	4.8	8.8	—	1.8	—	102	—	2.3	1.8	—
3	5	—	1.9	1.7	4.2	7.1	0.9	1.1	66	—	0.7	1.4	1.5	3
	6a	—	2.2	1.8	4.1	5.2	1.0	—	—	—	—	2.6	—	9
4	7	16	2.2	1.5	4.2	9.0	0.2	0.2	4	5	—	3.9	0.9	9
5	8	16	2.2	1.7	4.6	8.0	0.1	0.2	3	5	—	2.7	0.9	9
6	9	15	2.2	1.5	5.1	7.5	0.2	0.1	4	3	—	4.0	1.0	10
7	10-14	9	1.8	1.6	3.7	6.6	0.2	0.1	4.2	3.0	—	3.3	0.8	9.2
8	15-18	12	2.1	1.7	4.1	7.5	0.2	0.2	4.7	4.8	—	3.4	0.8	10
5-8	19-27	13	2.1	1.6	4.3	7.6	—	—	—	—	—	3.4	0.8	9.3
9	28	16	2.4	1.7	4.4	9.0	1.9	1.7	ca. 150	ca. 120	0.8	2.7	1.1	10
10	29	9	2.0	1.6	3.5	6.5	0.2	—	4	—	—	4.1	0.7	10
11	30-35	13	2.0	1.7	4.3	7.8	0.1	0.1	4.3	4.8	—	3.5	0.8	9.0
12	36-40	15	2.0	1.6	4.5	8.4	0.2	0.1	4.0	4.0	—	3.6	0.9	9.0
13	41-42	13	1.9	1.6	4.0	8.0	0.1	0.2	3.0	3.5	—	2.9	1.0	9.5
14	43	17	2.2	2.1	4.5	7.7	1.3	1.0	83	71	1.0	2.5	1.4	5
15	44	15	2.1	1.6	4.3	8.0	0.4	0.8	28	43	1.1	2.7	1.1	9
16	45	12	2.0	1.7	4.5	7.5	0.5	0.4	46	32	0.4	3.6	0.9	9
	46	19	2.0	1.7	5.2	10.0	0.8	0.4	53	27	0.6	2.2	0.9	8
	47-51	15	2.1	1.9	4.5	8.0	0.2	0.1	5.0	4.0	—	3.4	1.1	8.4
Normal Queens	Means	20.5	2.6	2.0	5.0	9.6	2.0	2.0	165	165	1.1	2.1	2.2	2.6
	Ranges	17-25	2.4-2.8	1.9-2.3	4.6-5.3	8.0-12.0	1.4-2.4	1.6-2.6	129-197	116-217	1.0-1.3	1.2-2.6	1.8-2.7	2-5
Normal Workers	Means	10.4	2.1	1.7	4.4	7.0	0.16	0.16	3.3	3.2	—	4.0	1.0	9.1
	Ranges	8-14	2.0-2.4	1.6-1.9	4.0-4.7	6.0-8.0	.05-.32	.05-.29	1-8	1-9	—	3.3-4.3	0.7-1.4	8-11

Dead late in nuptial stadium

Two adults were produced by this technique. Several measurements of these bees are given in Table I under treatment 1, bees 1 and 2. The left ovary of bee 2 was destroyed during dissection. It will be noted that, in comparison to the means and ranges of measurements of normal queens and normal workers, these bees were queen-like in every characteristic measured. General observations indicated that in body shape and color, form of mandibles, and form and chaetotaxy of metathoracic legs, these bees were queen-like; they were not worker-like in any characteristic observed.

Larvae were also reared in glass cells in a constant temperature cabinet. Every 2 hours royal jelly was pipetted directly from queen cells into the glass cells containing larvae of about the same age. One adult and one virtually mature pupa were produced by this technique. Their measurements are given in Table I, treatment 2, bees 3 and 4. These bees were queen-like in every characteristic observed. The right ovary of the pupa was too degenerate for an exact measurement, but it was approximately the same size as the left ovary.

Three pupae reared by these techniques differentiated sufficiently before death so that some of their characteristics could be evaluated. One of them appeared to be queen-like in the few characteristics which could be observed; the others were intermediate in tongue lengths, sizes of abdomens and spermathecae, and had worker-like metathoracic legs.

### STORED ROYAL JELLY

Royal jelly was removed from queen cells daily and refrigerated at about 5°C for 1 to 4 weeks. This royal jelly was fed every 2 hours to larvae in glass cells in a constant temperature cabinet. The larvae were fed on royal jelly that was taken from cells containing larvae within about 1 day of their own age. Well over half of the larvae fed by this technique died within a day after the feeding regimen began. Of more than 100 larvae, only 1 lived until it was adult, and another lived until late in the pupal stadium. The measurements of these bees are given in Table I, treatment 3, bees 5 and 6. Both were intermediate between queens and workers. The mandibles of the adult had slight indentations and thus were intermediate in form; the body shape was worker-like; the metathoracic legs were worker-like in chaetotaxy. The pupa had worker-like mandibles and metathoracic legs, but the abdomen was queen-like in shape.

In an attempt to develop easier, more efficient rearing methods, several types of containers and feeding techniques were tested. In the method finally adopted, royal jelly was spread about 2 or 3 mm deep over the bottom of a petri dish, and 5 or 10 larvae were placed in it. In the first experiment a ball of dampened cotton was also placed in the petri dish. The larvae were left in the food until they had spun padlike cocoons upon which they rested, and then they were transferred to clean petri dishes to pupate.

Royal jelly that had been stored at about 5°C for slightly more than a year was used in developing and testing this technique. The jelly had been removed from queen cells only on the fourth day after larvae were grafted into them, and it was fed to larvae both with and without modifications. All of the bees reared on this jelly were predominantly worker-like in their characteristics, but there were some variations among them that resulted from modifications that were performed on their food. In treatment 4, a dish of unmodified jelly was taken from the refrigerator each day, and the larvae were transferred to it. Bee 7 was reared on this jelly. Larvae also were fed by the same technique on royal jelly from the same source that had been diluted 10 and 20 per cent with water (treatments 5, bee 8, and treatment 6, bee 9, respectively). Other petri dishes of jelly were placed in the laboratory window and exposed to light and heat for two days; this jelly attained the consistency of a heavy paste, was slightly brown in color, and had an unpleasant odor. Bees 10 through 14 were reared on this royal jelly. When larvae were transferred to fresh dishes of food, other larvae were reared in the dishes from which they had been removed. These larvae were left in the same dish of food until ready to pupate. By this technique, adults developed only on the jelly that had been diluted with water (treatment 8). One or both ovaries could not be found in many of the bees reared by these treatments. The means of the remainder of their measurements are given in Table I, bees 19 through 27. The bees that developed



on the drier royal jelly had smaller abdomens, and weighed less than the bees that developed on the more dilute jelly, but there were no other consistent differences in the bees from different treatments. Of the 19 adults and 4 mature pupae reared on this one-year-old royal jelly by all methods, 3 had spermatheca 0.1, 0.2, and 0.3 mm across. Three had tongue measurements within the range of variation of the group of normal queens shown in Table I, and 6 had tongues that were intermediate in length between those of normal queens and normal workers. None of these bees had basitarsi that were queen-like in any way, but 4 had shorter basitarsi, and 6 had lower basitarsal indices than those of any of the normal workers.

The large size and heavy weight of the bees reared on the more dilute royal jelly seemed to be due to extensive fat bodies distributed throughout the abdomen. In many of these bees the ovaries and oviducts were partially or completely embedded in the fat bodies, and in separating the fat bodies to search for them, some of the ovaries may have been destroyed. In a few instances it is known that the ovaries were absent. A few bees had oviducts with thick, chitinous appearing walls that terminated in a long, spine-like extension. This "spine" often was partially surrounded by scattered cells, possibly held in place by tracheae that enwrapped sections of it. An occasional oviduct that appeared to be completely normal terminated in a well developed calyx that had what appeared to be a tiny, twisted, under-developed ovariole appressed to its surface.

Royal jelly was collected from queen cells on the second day after they were grafted, and on each day thereafter. The jelly from larvae of the same age was stored in the same container under  $\text{CO}_2$  at  $5^\circ\text{C}$  for about two weeks, and then was fed to larvae in petri dishes in the constant temperature cabinet. Each day the larvae were transferred to royal jelly that had been taken from queen larvae of approximately their own age. The measurements of the one adult that developed is shown in Table I under treatment 9, bee 28. It will be noted that this bee was worker-like or intermediate in most characteristics, but in weight and in size of abdomen, ovaries, and spermatheca, she was rather queen-like. A few of the ovarioles were fused with each other so that an exact count was impossible. A pupa produced in the same treatment appeared to be worker-like in all characteristics except weight and breadth of abdomen.

Larvae were reared in the food from which those in treatment 9 had just been removed, and by the same technique. This jelly was slightly desiccated and had been held at  $34^\circ\text{C}$  for 24 hours when the larvae were placed in it. The one adult that developed (bee 29, treatment 10), was worker-like in all characteristics. The left ovary could not be found, but it is not certain that it was absent.

About a year later, the royal jelly that had not been required for treatments 9 and 10 was used in another feeding experiment; this jelly had been held under  $\text{CO}_2$  at  $5^\circ\text{C}$  for a year. During prolonged storage, many hard, white, crystal-like bodies form in royal jelly. These bodies are insoluble in all of the solvents that have been tested, but they will disperse in the royal jelly if it is stirred sufficiently. One group of larvae was reared on jelly in which the crystal-like bodies had been dispersed, (treatment 11), while another group was reared on the jelly in which the bodies were present (treatment 12). The larvae were transferred daily to food from larvae of approximately their own age. The means of the measurements of these bees are shown in Table I. There were no consistent differences between the bees in the different treatments. The 2 largest of these bees each weighed 18 cg. The length of the tongue of one of the bees was barely within the range of variation of tongue-length of normal queens; the same bee had 22 ovarioles in both ovaries, and a spermatheca 0.5 mm across. Three other bees had spermatheca 0.8, 0.6, and 0.4 mm across. Three bees, rather than being queen-like, had shorter basitarsi than any of the normal workers, and 3 had lower basitarsal indices.

Each day the larvae in treatments 11 and 12 were transferred to fresh dishes of jelly, the royal jelly from which they were removed was used to rear additional larvae that were left in the same dish of food until ready to pupate. One adult and one fairly mature pupa developed on the jelly that had been taken from queen cells on the second day after they were grafted. This was the royal jelly from treatment 12, which contained crystal-like bodies. The adult was unusually large, and the pupa had a queen-like

tongue, but both were workers in other respects. The means of their measurements are given under treatment 13, Table I.

One adult developed on each of the dishes of royal jelly taken from queen cells on the third day after grafting. This was the jelly given to queen larvae by the nurse bees during parts of the third and fourth days of larval life. Bee 43, Table I was produced on the jelly in which the crystals had been dispersed. This individual was slightly queen-like or intermediate in most characteristics, as can be seen from her measurements. This was also true of the characteristics that could not be measured. Her coloration and mandibles were queen-like, and the chaetotaxy of her metathoracic leg was intermediate between that of typical queens and typical workers; there was a pollen basket fringed by slender setae, and with scattered setae in it. Bee 44, Table I developed on the royal jelly that had not had the crystal-like bodies dispersed. This individual had a queen-like spermatheca, a rather short tongue, and ovaries that were intermediate in size; she was worker-like in her other characteristics. Two other individuals lived until fairly late in the pupal stadium. One had a short tongue and a slender abdomen much like that of a very small queen, but both were worker-like in other characteristics, and both had unusually short basitarsi.

### EXTRACTS OF ROYAL JELLY

The ultimate objective of these experiments is to determine the nutritional factors responsible for the differentiation of castes of the female honeybee. In order to accomplish this, it will be necessary to rear larvae on a chemically controlled diet in the laboratory. The best chemically controlled diet that has been developed will not support development from egg to adult. In a preliminary experiment, both the ether soluble and the total water soluble fractions of royal jelly were added to the best of the diets that had then been developed; the carbohydrate was omitted from the diet for this test. The royal jelly was more than a year old at the time these extracts were made, so no special techniques were employed to preserve highly labile biologically active substances. Bees 45, 46, and 47 through 51 developed on this diet. It will be noted that bee 45 had spermatheca and ovaries much larger than those of normal workers. Bee 46 had these features and a queen-like tongue. Both had small, queen-like pharyngeal glands. Two other bees had tongues intermediate in length between those of normal queens and normal workers, but except in weight and body size, all of the other bees were worker-like.

Other bees that are normal workers in their essential characteristics have been reared on the chemically controlled diet to which extracts of royal jelly have been added, but the fraction of jelly that contains the nutrient that is missing from the diet, and the one that contains the substance necessary for the differentiation of queens, has not been definitely established.

### GENERAL DISCUSSION

It is obvious from these experiments that there is a rather labile substance, or substances, in royal jelly that initiates or controls the differentiation of queens, or that upon storage some part of the royal jelly undergoes a change which prevents the differentiation of queens. The former possibility seems to be the more likely, though there is some evidence to suggest that the latter explanation may be of some importance. Young worker larvae that are fed in the laboratory on stored royal jelly taken from queen cells containing larvae less than 3 days old grow more slowly and have a higher mortality rate than similar larvae fed on royal jelly taken from older queen larvae. It is not known how the nurse bees could vary the composition of royal jelly with the age of the larvae being fed, but because of the technique used in this study, it is believed that differences in the composition of the food of younger and older queen larvae are responsible for the differences in the response of larvae to the food. Other evidence on this question has been discussed in some detail by Ribbands (1953).

These and other experiments also suggest that a partial change in the developmental physiology from worker toward the queen-type, is rather lethal, and that among the adults that emerge, the anatomically most extreme forms that are viable often develop. The bees without ovaries, and the bees with unusually short basitarsi are examples

of such extreme forms. These and other aspects of dimorphism in the female honeybee have been discussed more fully by Weaver (1957).

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# Major Pollen Sources in the Manhattan, Kansas, Area and the Influence of Weather Factors Upon Pollen Collection by Honeybees<sup>1</sup>

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## ABSTRACT

*The study of the pollen sources in a region is of importance to beekeeping management as it helps to determine whether the area is a good or poor beekeeping district. Weather factors were studied since they have considerable influence upon plant growth, bloom yield of pollen, the activity of bees in pollen collection and the quantities of pollen gathered.*

*Pollen was trapped from overwintered colonies in 1954 and 1955. Microscopical examination was made for identification. Forty-nine plants were found to be used by the bees for pollen collection through the active season. The major pollen sources in the early spring were soft maple, elms, dandelion, boxelder, and redbud. Willow, spiraea, honeysuckle, black and honey locusts were main sources in the late spring. During the summer, yellow and white sweet clovers, alfalfa and corn were the major pollen sources. Smartweed, sunflower and sorghum were the principal autumn sources. There was an increase in percentage of total weight of pollen collected for the season during March, April, and May, with that for May being the greatest of the season. Another increase occurred from June through September, with that for August and September each being nearly as great as that for May.*

*Flight activity of bees and pollen collection increased on warm sunny days during the early spring. High temperatures and drought affect plant growth and bloom, causing a decrease in pollen collection. Good yields of pollen followed rainfall which occurred after a period of hot dry weather.*

## INTRODUCTION

Pollen is an important source of proteins, minerals, enzymes, and vitamins in the honeybee diet and is also an important factor in brood rearing. This essential food of bees is important in the production of large colony populations in spring and autumn for nectar collection in honey production and wintering, respectively. Pollen stored in combs is especially important in late winter and early spring for brood rearing before plants bloom. Early spring in the northern hemisphere at the time of plant bloom is subjected to cold and rainy days that interfere with flight and pollen collection. Parker (1926) noted that brood rearing is limited to periods when pollen is available in the field and that it ceases completely in the absence of pollen. Betts (1928) stated that studying the pollen sources and constructing a pollen species curve for different localities is important to the bee-keeping industry. She also emphasized the importance of pollen for brood rearing.

Studies of the pollen cycle, and the availability of pollen during the active season, and the different plants which furnish pollen have been made by many workers in different localities, but still more information is needed. Prior reports have been based primarily upon field observations and bees caught collecting pollen from certain plants, and upon the pollen loads carried by bees returning to the hive (Parker, 1926; Betts, 1928; and Percival, 1947). Todd and Bishop (1940) studied the seasonal distribution of pollen collections in four locations in California. During the complete season, the pollen trapped ranged from about 13.5 to 18.0 kilograms per colony. Eckert (1942) used several pollen traps to determine the quantities of pollen required by a colony. He stated that a normal colony of honeybees may collect as much as 122.24 pounds of

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pollen in a single season at Davis, Calif. He also identified the various types of pollen collected to determine the relative importance of each plant as a pollen source. Synge (1947) used two pollen traps in two hives at Rothamsted Experiment Station. She analyzed both quantitatively and qualitatively the daily collection of the pollen as to species.

The color of the pollen pellets in relation to plant sources and the factors causing the color variations were studied by Reiter (1947) and Hodges (1949, 1952). The color of the pollen pellets was taken as a partial basis for identification by Parker (1922), Betts (1935), Todd and Bretherick (1942), Percival (1947), Synge (1947), and Vansell and Todd (1949).

Weather is a complicated factor that influences flight activity of the bees, colony strength, plant growth, and bloom. Lundie (1925) stated that the lowest temperature at which flight began was 50° F. and that during hot days flight activity decreased. Parker (1926) noted that the availability of pollen was influenced by relative humidity and temperature. Todd and Bishop (1940) stated that the peaks in quantities of pollen gathered by bees were correlated with the blooming of good plant sources and not with the peak of the colony population. They noted that the dehiscence of the anthers was affected by atmospheric conditions and that the quantities of pollen collected were influenced by cold, rain, or cloudiness. The effect of weather conditions on pollen availability and pollen collection was studied also by Percival (1947) and Synge (1947).

### PROCEDURE

Trapping pollen from three colonies began in March and ended in October during each of the years 1954 and 1955. The pollen traps used have the same principle of operation as that used by Schaefer and Farrar (1946) except that the bees pass through only one grid. Bees on entering the hives must pass through an upper grid of five meshes to the inch, which scrapes off the pollen pellets. The pellets then fall through the lower grid into the pollen tray.

There was no appreciable difference in the sources constituting the pollen collected by the three different colonies as indicated by color of the pollen pellets. Microscopical examinations were limited to the pollen collected by Colony A in 1954. The daily collection of pollen was weighed, and a representative sample was taken for analysis. When the weight of the pollen trapped was 20 grams or less, the whole quantity was taken for further examination. When weight ranged between 20 to 100 grams, 20 per cent of the quantity was examined; if more than 100 grams, 4 per cent of the total pollen trapped was examined. Samples were then sorted, separating the different colors by using an aspirator collection tube. Texture, size, and shape of the pellets were also of some help in sorting. The homogenous pellets were weighed and multiplied by the proportion of each type of pollen present.

A representative sample of each type of pollen pellets was taken for the microscopical examination. Two methods were used for preparing microscopical slides. A minute portion of a selected pollen pellet was placed on a slide and a drop of 95 per cent alcohol was added and well stirred. In the first method, after washing out the oily resins of the pollen with 95 per cent alcohol on the slides, the pollen was stained with alcoholic basic fuchsin. The excess stain was washed out with 95 per cent alcohol. After drying the pollen mount, a drop of Xylol was added to the mass for clearing, and this was followed by a drop of the mounting medium (Permount), over which a cover glass was placed. Although this method caused the pollen grains to shrink and rupture, the identifying sculptures or spines on the exine, however, were still clearly defined.

To study the dimensions and other characters of the grains, and for immediate examination, the method used by Owczarzak (1952) was followed. The oily resinous substances were washed out of the pollen grains with 95 per cent alcohol, after which hot drops of glycerine jelly stained with methyl green and phloxine were added and then covered with a cover glass. The immediate examination of the slides prepared by this second method was satisfactory; but, if preparations were left a few weeks, the intine of the grains became more deeply stained by absorbing more of the dye.



Identification was made either by comparison with slides prepared from pollen grains obtained from the flowering plants or with slides prepared from pollen pellets of bees caught while working on known plants. Descriptions and drawings noted in other papers also were used for identification.

## RESULTS

Activity in pollen collection began in early spring as soon as the soft maple and the elm began to bloom. Total quantities of pollen trapped during the seasons of 1954 and 1955 are shown in Table I.

TABLE I — Total Quantities of Pollen, in Grams, Collected from Colonies A, B, and C During the Years 1954 and 1955, Manhattan, Kansas.

	1954			1955		
	A	B	C	A	B	C
March	728.80	—	—	9.8	—	—
April	1,933.20	1,464.1	1,662.4	1,314.68	1,338.15	572.0
May	2,348.20	3,906.20	2,996.7	1,089.40	1,831.7	1,303.1
June	465.27*	2,287.20	1,982.78	1,260.42	1,720.40	1,096.80
July	1,174.35	3,330.27	1,610.88	1,062.94	759.	336.99
August	2,190.94	3,274.80	1,814.90	4,359.36	1,640.42	1,194.87
September	2,133.95	1,148.55	1,356.18	2,089.63	1,009.20	706.84
October	70.35	23.30	24.65	124.19	76.05	41.9
Total	11,045.08	15,434.42	11,448.49	11,310.42	8,374.92	5,252.5

\* The colony was queenless for about two weeks during May.

Forty-nine plants were found to furnish pollen, of which 30 were identified (Figs. 1 and 2).

### MAJOR SOURCES OF POLLEN

The major sources of pollen were found to be the same during both years. Plants yielded pollen from March 6 to October 12, 1954, and from March 12 to October 25, 1955. Variations occurred in blooming dates and in the quantities of pollen collected from each source. Such variations were caused by weather factors and available moisture in the soil. A summary of the 1954 and 1955 blooming periods, the quantities of pollen obtained from each type of plant, and their relative importance is presented in Table II and Figs. 1, 2, and 6.

### SOURCES OF POLLEN DURING SPRING

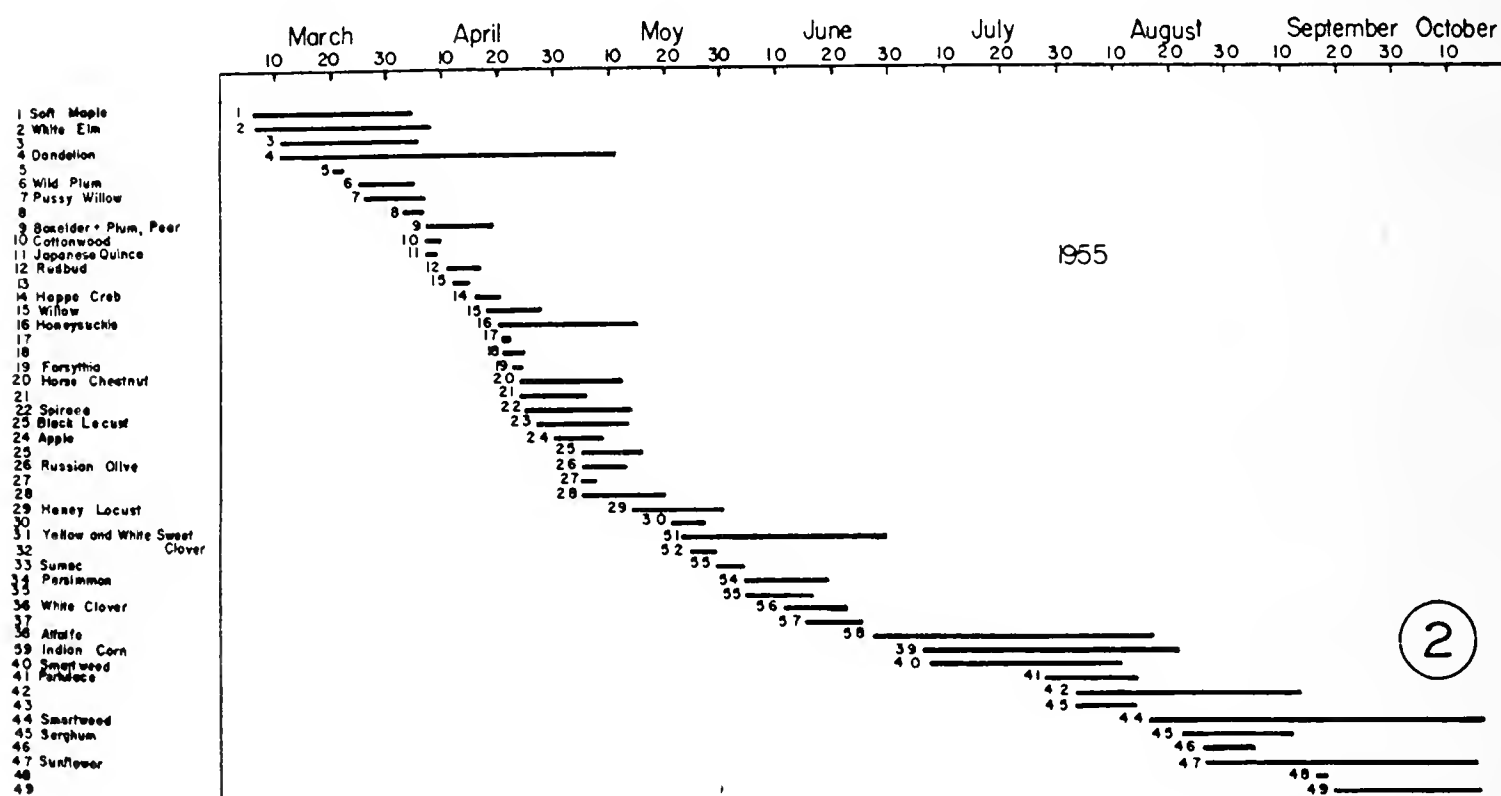
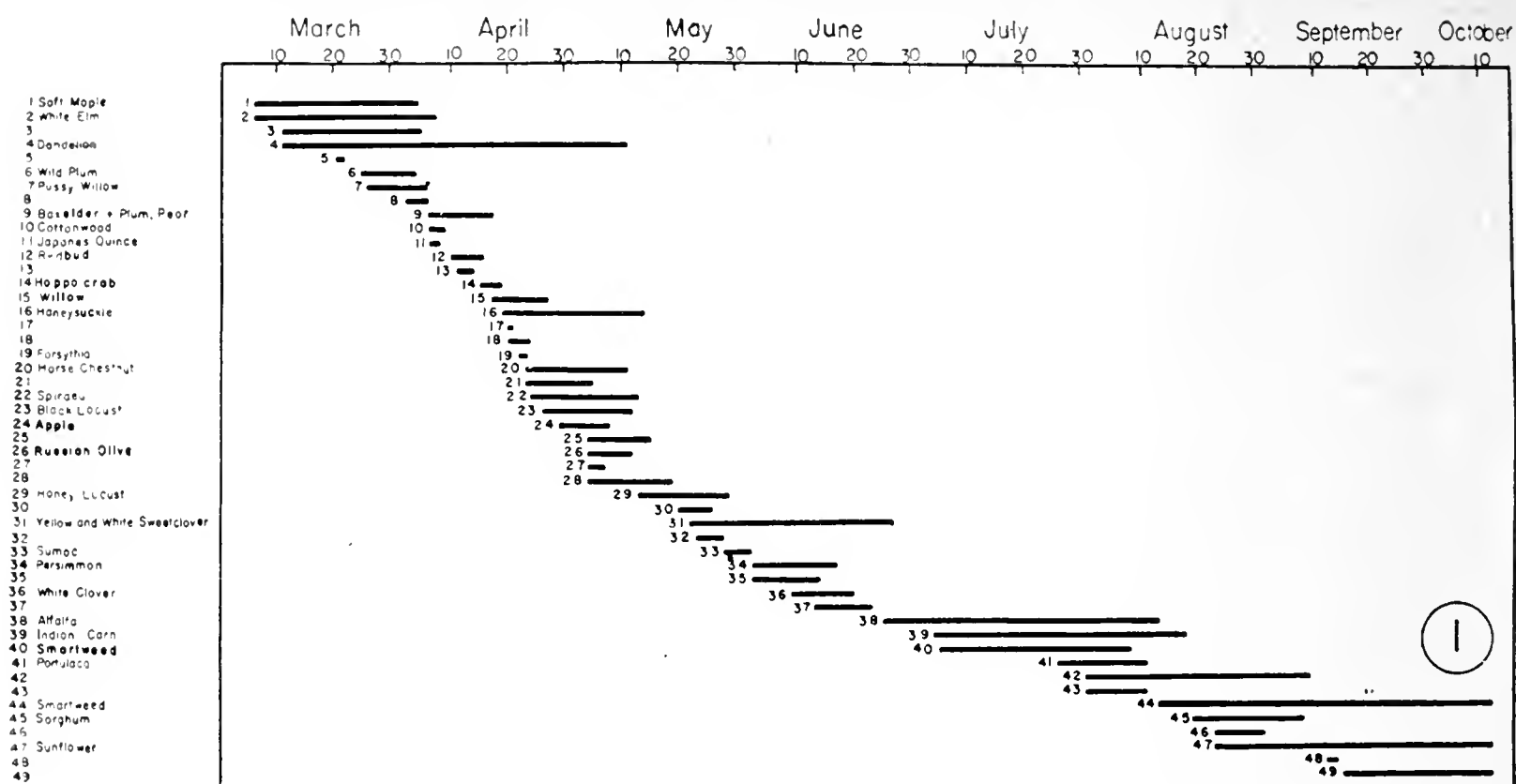
During the early spring, the principal pollen sources were forest and shade trees followed by the bloom of shrubs, ornamental, and fruit trees. This period extends from March 1 to June 1. The major species included in this category were:

*Acer saccharinum* L., soft maple. This tree blooms early in the spring and furnishes large quantities of pollen at a critical period in the colony development and management. Soft maple pollen aids tremendously in increasing the population within the colony. Favorable weather conditions are important in its blooming as well as in bee flight and pollen collection. On a warm clear day in March, 1954, the quantity of pollen trapped from one colony from this source was 217.65 grams.

*Ulmus americana* L., American or white elm. The blooming period of the elm overlaps with that of the soft maple. The bees were more constant in working the soft maple than the elm. The activity of the bees working on this plant was also influenced by weather conditions.

*Taraxacum officinale* Weber., dandelion. This plant grows as a weed. During cool weather it had a long blooming period extending from March until May. In the early period, the activity of the bees was subjected to unfavorable weather factors which determine the daily quantities of pollen gathered.

*Salix* spp., willow. Three species of willow of importance to bees are found in this region. *S. discolor* Muhl., pussy willow, blooms early in the spring and is considered a



Figs. 1-2. Periods of pollen collection from different plants. Fig. 1, 1954. Fig. 2, 1955.

minor source of pollen because of the small number of plants growing in this area. The other two species are *S. interior* Rowlee, sandbar willow, and *S. amygdaloides* Anders., peach-leaved willow.

*Acer negundo* L., boxelder. This plant is abundant in this area and is a good source of pollen. The beginning of its bloom followed that of soft maple and elms. Other plants blooming during this period were comparatively scarce, which resulted in the bees concentrating on the boxelder. During the latter part of the blooming period of boxelder many plants belonging to the family Rosaceae, especially plum and pear trees, began to bloom.

*Cercis canadensis* L., redbud. Redbud is considered to be a good source of pollen. It is commonly found on hillsides and along the borders of streams.

*Lonicera* spp., honeysuckle. Many species of this genus are distributed in this area, especially *L. tartarica* L., tartarian honeysuckle, an ornamental shrub. It furnished good quantities of pollen during late spring.

*Spiraea vanhouttei* Zabel., spiraea. This flowering, ornamental shrub provided good quantities of pollen through late spring.

*Robinia pseudoacacia* L., black locust, and *Gleditsia triacanthos* L., honey locust. Both species were important sources in late spring despite their short blooming period.

TABLE II — Weights and Percentage of Pollen Collected from Different Plants Through the 1954 Active Season and the Periods in which Pollen was Collected, Manhattan, Kansas.

Plant No.	Plant name	Grams	% of total season	Time of pollen collection			
SPRING — MARCH 1 to JUNE 1							
1	<i>Acer saccharinum</i> L. (soft maple)	649.4	6.1	March 6	—	April 4	
2	<i>Ulmus americana</i> L. (white elm)	130.04	1.2	March 6	—	April 7	
3		32.62	0.3	March 11	—	April 5	
4	<i>Taraxacum officinalis</i> Weber. (dandelion)	123.76	1.1	March 11	—	May 11	
5		0.15	0.001	March 21	—	March 22	
6	<i>Prunus angustifolia</i> Marsh. (wild plum) and	35.95	0.3	March 25	—	April 4	
7	<i>Salix discolor</i> Muhl. (pussy willow)	17.15	0.16	March 26	—	April 6	
8		1.55	0.01	April 2	—	April 6	
9	<i>Acer negundo</i> L. (boxelder) and <i>Prunus</i> sp. and † <i>Pyrus</i> sp.	344.25	3.27	April 6	—	April 18	
10	<i>Populus deltoides</i> Marsh. (cottonwood)	41.50	0.39	April 6	—	April 9	
11	<i>Chaenomeles lagenaria</i> (Japanese quince)*	26.0	0.24	April 6	—	April 8	
12	<i>Cercis canadensis</i> L. (redbud)	186.35	1.77	April 10	—	April 16	
13		24.5	0.23	April 11	—	April 14	
14	<i>Pyrus</i> sp. (Hoppa crab)†	49.0	0.46	April 15	—	April 19	
15	<i>Salix</i> spp. (willow)†	156.72	1.49	April 17	—	April 25	
16	<i>Lonicera</i> spp. (honeysuckle)*	290.78	2.76	April 19	—	May 14	
17		25.0	0.23	April 20			
18		12.3	0.11	April 20	—	April 24	
19	<i>Forsythia</i> sp. (forsythia)†	14.25	0.13	April 22	—	April 23	
20	<i>Aesculus glabra</i> Willd. (Ohio buckeye)	52.0	0.49	April 23	—	May 11	
21		2.25	0.02	April 23	—	May 5	
22	<i>Spiraea vanhouttei</i> Zabel (spiraea)	219.95	2.09	April 24	—	May 13	
23	<i>Robina pseudoacacia</i> L. (black locust)	570.98	5.43	April 26	—	May 12	
24	<i>Pyrus malus</i> L. (apple)*	35.10	0.33	April 29	—	May 8	
25		184.55	1.75	May 4	—	May 15	
26	<i>Elaeagnus angustifolia</i> L. (Russian olive)*	26.55	0.25	May 4	—	May 12	
27		1.65	0.01	May 4	—	May 8	
28		25.65	0.24	May 4	—	May 20	
29	<i>Gleditsia triacanthos</i> L. (honey locust)*	767.25	7.3	May 13	—	May 29	
30		29.35	0.27	May 20	—	May 26	
SUMMER — JUNE 1 to SEPTEMBER 1							
31	<i>Melilotus officinalis</i> Lam. and <i>M. alba</i> Desf. (y. and w. sweet clover)	793.21	7.54	May 22	—	June 27	
32		2.0	0.019	May 23	—	May 28	
33	<i>Rhus glabra</i> L. (sumac)*	1.55	0.014	May 28	—	June 2	
34	<i>Diospyros virginiana</i> L. (persimmon)*	39.78	0.37	June 2	—	June 17	
35		6.85	0.065	June 2	—	June 14	
36	<i>Trifolium repens</i> L. (white clover)	22.34	0.21	June 9	—	June 20	
37		3.72	0.03	June 13	—	June 23	
38	<i>Medicago sativa</i> L. (alfalfa)	175.75	1.67	June 25	—	Aug. 13	
39	<i>Zea mays</i> L. (Indian corn)	1,517.56	14.44	July 4	—	Aug. 18	
40	<i>Polygonum persicaria</i> L. (smartweed)*	12.49	0.118	July 5	—	Aug. 11	
41	<i>Portulaca</i> sp. (purslane)	1.45	0.013	July 26	—	Aug. 11	
42		162.67	1.54	Aug. 1	—	Sept. 7	
43		9.40	0.08	Aug. 1	—	Aug. 11	
AUTUMN — SEPTEMBER 1 to OCTOBER 15 or 30							
44	<i>Polygonum</i> spp. (smartweed)	2,484.82	23.64	Aug. 13	—	Oct. 12	
45	<i>Sorghum vulgare</i> Pers. (sorghum)	354.45	3.37	Aug. 19	—	Sept. 8	
46		16.75	0.15	Aug. 23	—	Sept. 1	
47	<i>Helianthus annuus</i> L. (sunflower)	698.20	6.64	Aug. 23	—	Oct. 12	
48		6.50	0.061	Sept. 12	—	Sept. 14	
49		122.8	1.16	Sept. 15	—	Oct. 12	

† Identified with the help of Dr. Roger P. Wodehouse.

\* Identified with the help of Dr. Ralph L. Parker from a file of pollen slides.

Other plants assume major importance during spring in other localities, but were of minor importance here because: (1) They were not abundant near the apiary; (2) their blooming period was short and subjected to unfavorable weather factors which lessened the activity of the bees; or (3) there were other competitive plants in bloom at the same time. Among this group were numerous Rosaceae. The similarity of the color and structure of the pollen pellets of fruit trees made it difficult to determine the source.

Fruit tree pollen species included *Prunus augustifolia* Marsh, Chickasaw or wild plum; *Chaenomeles lagenaria* Koidz, Japanese quince; *Pyrus* sp., Hoppa crab; and *Pyrus malus* L., apple. Minor sources included *Populus deltoides* Marsh, cottonwood; *Forsythia* sp.; *Aesculus glabra* Willd., Ohio buckeye; and *Elaeagnus augustifolia* L., Russian olive.

### SOURCES OF SUMMER POLLEN

The number of different kinds of pollen plants in the summer period (Table II, Figs. 1 and 2) was less than the spring period. This period extends from approximately June 1 to September 1. Sources of pollen were mostly from a few species with long blooming periods. Among these plants were also the major nectar-producing plants. At this time there were few other plants to compete with the major nectar-secreting and pollen-yielding plants.

Weather factors also exerted a marked influence on the plants in this period. Hot, dry weather which prevailed during certain periods, as well as low soil moisture, retarded the growth and the blooming of the plants and consequently the quantities of pollen collected decreased (Figs. 3 and 4).

*Melilotus officinalis* Lam. and *M. alba* Desf., yellow and white sweetclover. These two plants were widely distributed and furnished large quantities of pollen and were major sources of nectar. Similarity of color of the pollen pellets and morphology of the pollen grains made it difficult to separate the two species.

*Medicago sativa* L., alfalfa. This plant is a major nectar source. The availability of pollen extended over a long period, yet the daily quantity trapped was small.

*Zea mays* L., Indian corn. This important source of pollen during the late summer was reduced by hot, dry weather and low soil moisture content. A drought occurred during the latter part of June, 1954, and extended to the middle of July, but was ended by a heavy rain July 16; this was followed by a heavy yield of pollen from alfalfa, corn, and smartweed, but principally from corn July 18 (Figs. 3 and 4).

Minor sources during the summer period (Table II and Figs. 1, 2, and 6) were *Rhus glabra* L., sumac; *Diospyros virginiana* L., persimmon; *Trifolium repens* L., white clover; *Polygonum persicaria* L., smartweed; and *Portulaca* sp., purslane.

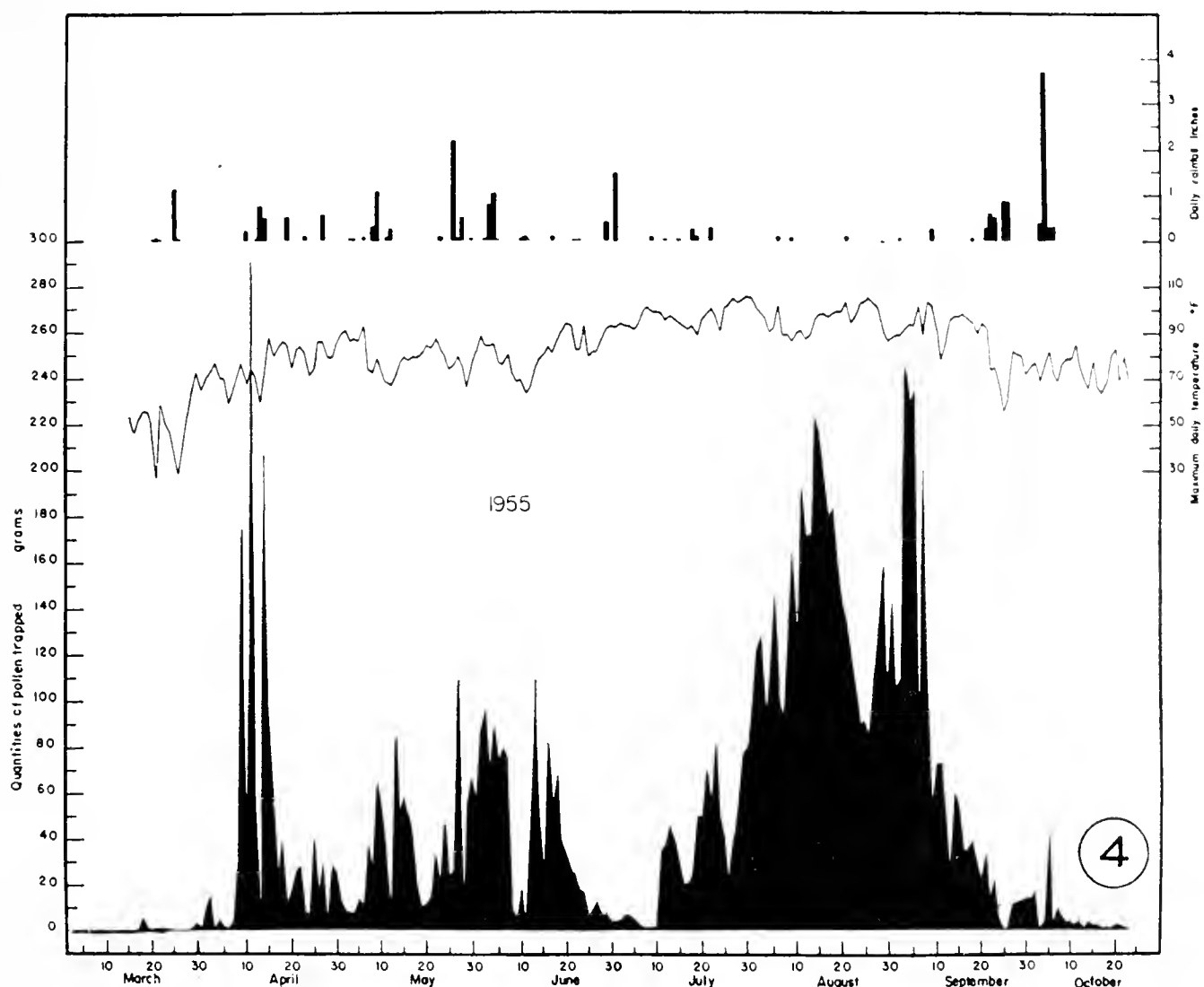
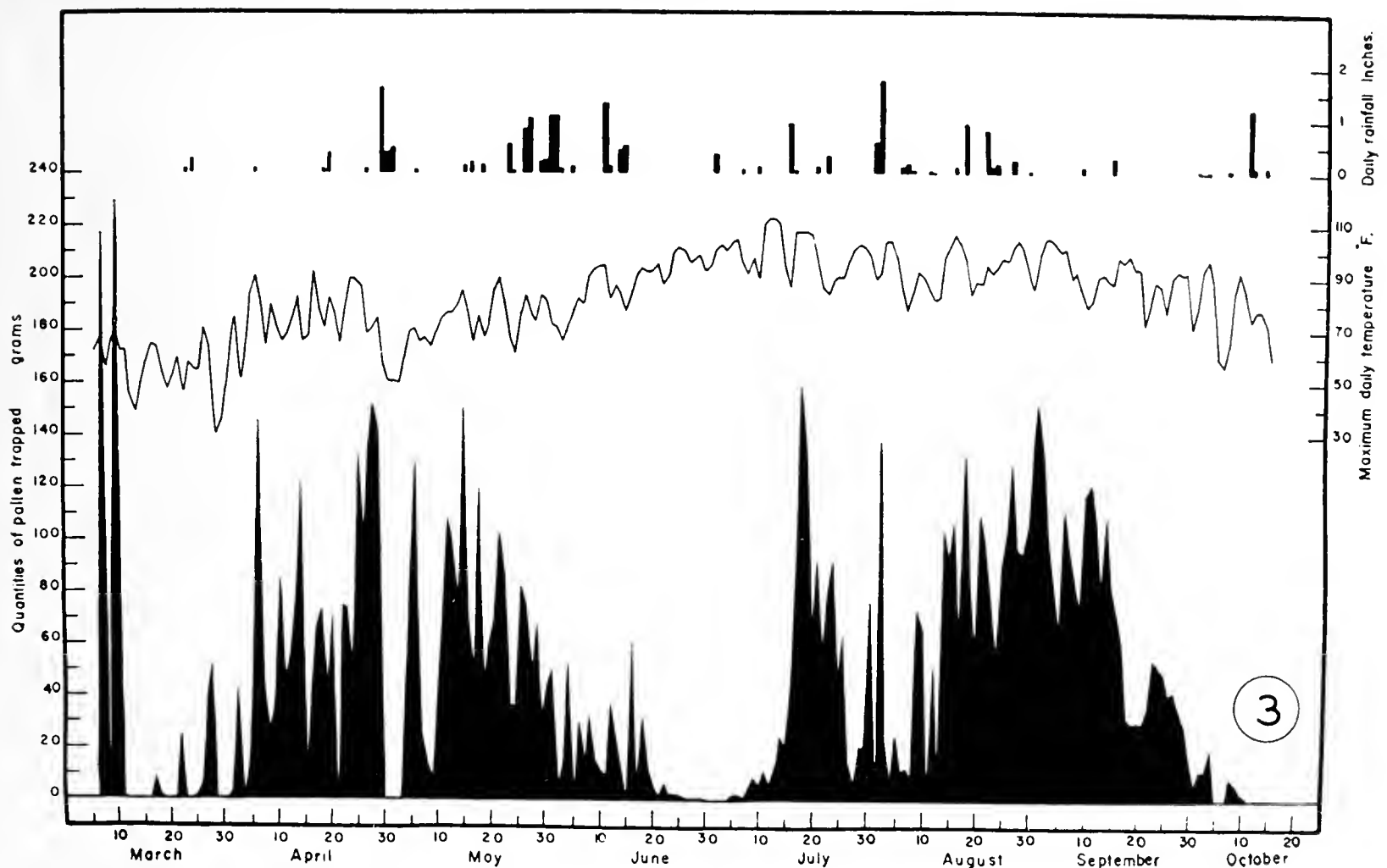
### SOURCES OF AUTUMN POLLEN

The group of plants included in this category blooms during the latter part of the summer as well as autumn, and consist mostly of weeds that grow along borders of the streams, roads, and in uncultivated fields. This period extends approximately from September 1 to October 25 or 30. The blooming period and quantities of pollen furnished were also influenced by hot, dry weather and low moisture content of the soil (Figs. 3 and 4).

*Polygonum lapathifolium* L., *P. persicaria* L., and *P. pennsylvanicum* L., smartweeds. The smartweeds are abundant in this area, growing as weeds in damp places and in poorly cultivated fields. The greatest quantity of pollen collected from any plant during the autumn was from smartweeds, attaining as much as 102.5 grams in one day.

*Sorghum vulgare* Pers., sorghum. This plant is widely cultivated and was worked eagerly by the bees in early morning. The quantity of pollen available from this plant is markedly influenced by weather factors and available soil moisture.

*Helianthus annuus* L., sunflower. Large numbers of sunflower plants grow as weeds on the hillsides, along the streams and roads, and in uncultivated fields. This is a good source of pollen until late in the fall.



Figs. 3-4. Total daily grams of pollen trapped. Maximum daily temperature and precipitation, March to October. Fig. 3, 1954. Fig. 4, 1955.

### WEATHER FACTORS

During early spring, flight activity and pollen collection of bees were limited to warm, sunny days. A sharp rise in the temperature was followed by a sharp rise in pollen collection as shown in Figs. 3 and 4. The maximum temperature March 7, 1954, was  $69^{\circ}$  F.; the quantity of pollen collected that day was 217.65 grams wholly from soft maple. March 8, unfavorable weather prevailed with a maximum daily temperature of  $56^{\circ}$  F. The temperature was unfavorable for bee flight and, consequently, no pollen was collected. March 9, the maximum temperature reached  $66^{\circ}$  F. and the quantity



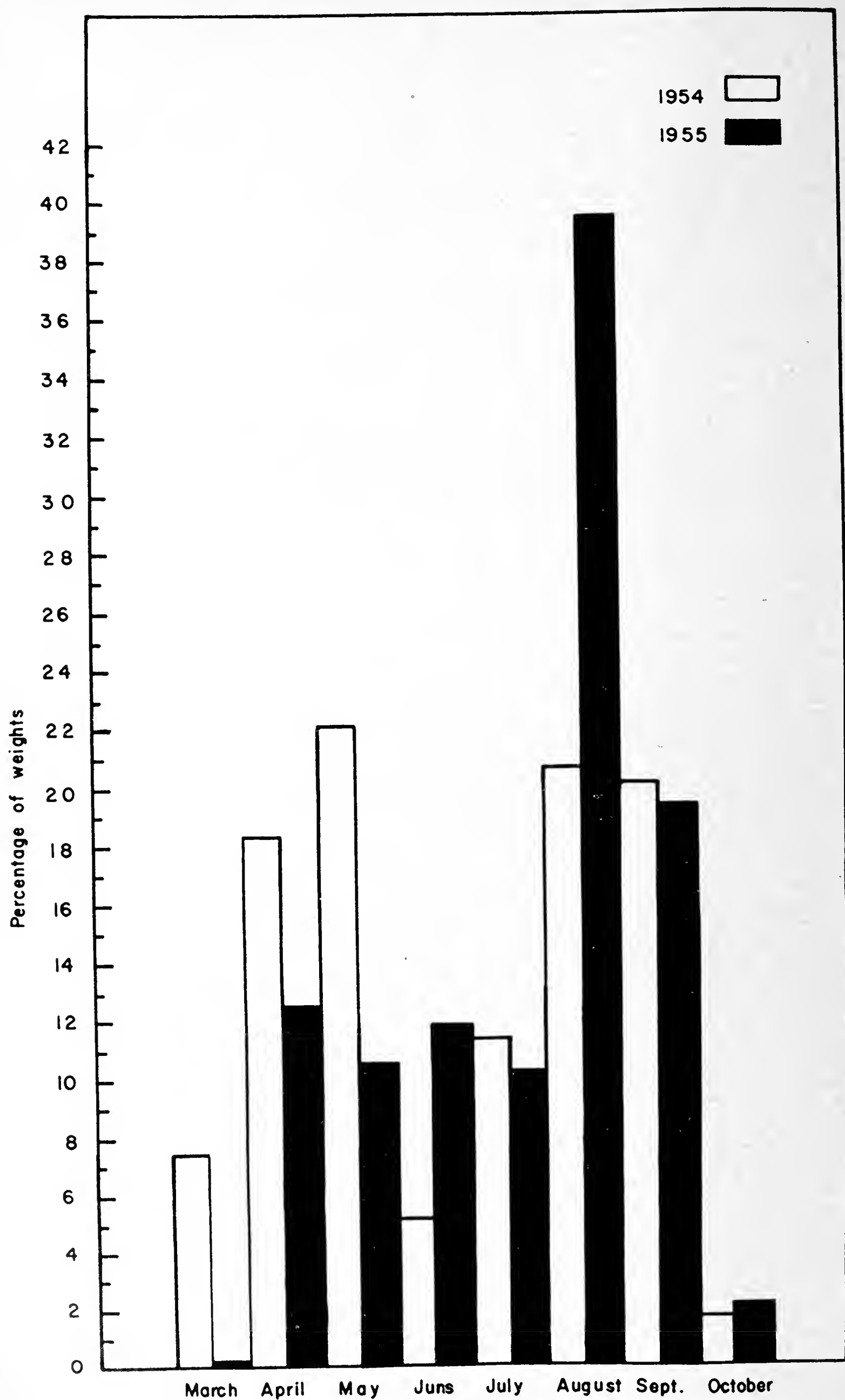


Fig. 5. Percentage of total pollen trapped from Colony A in different months during 1954 and 1955.

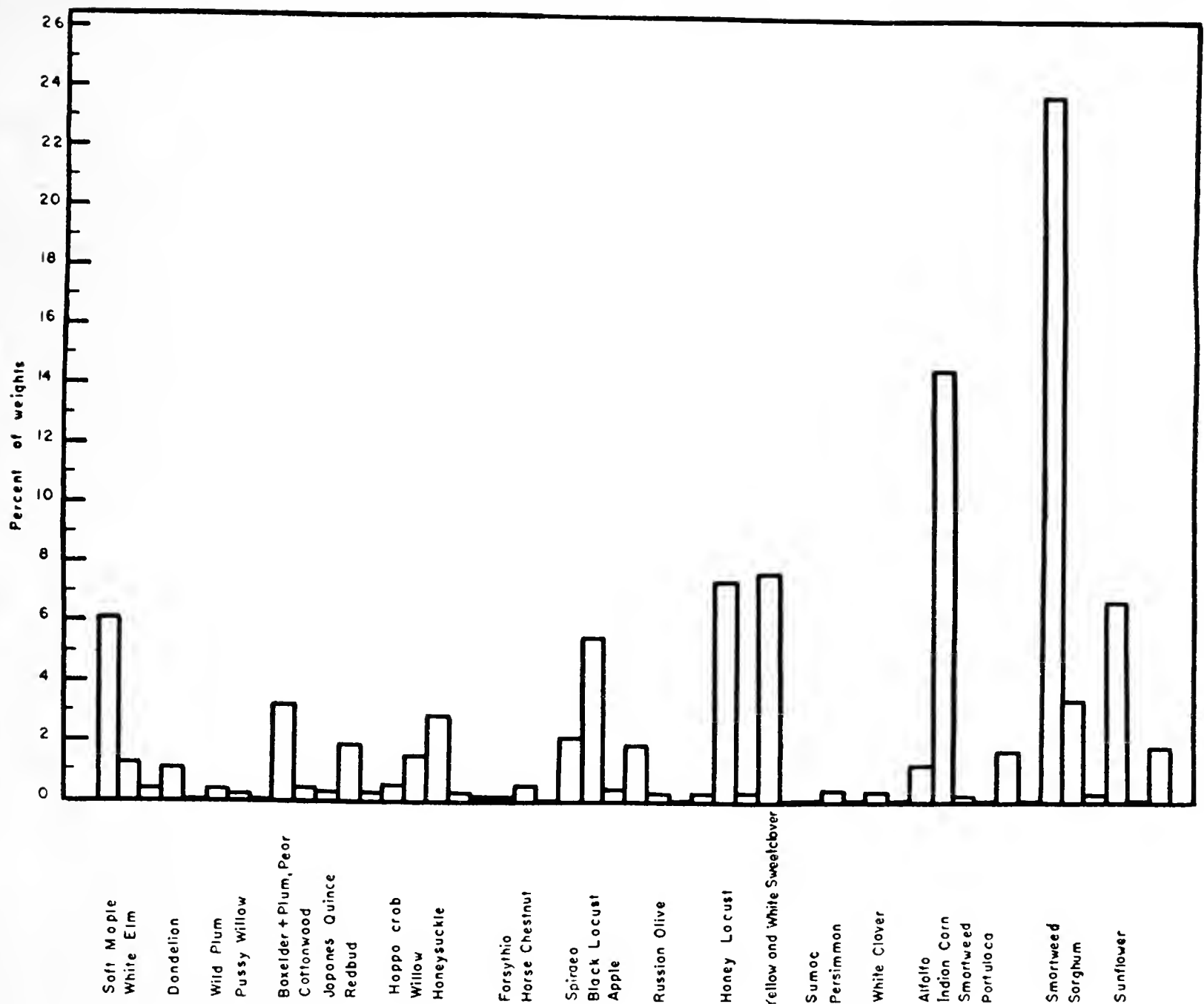


Fig. 6. Relative importance in percentage of different pollens trapped, 1954.

of pollen trapped was 128.7 grams. March 10, another rise in the temperature occurred with a maximum of 70° F., and the pollen trapped was 229.1 grams. These results show clearly the important role played by the weather in bee activity. If a period of bad weather covers the flowering period of a plant, it depresses flowering as well as bee activity.

Rainfall occurring during daylight hours hindered bee flight and resulted in a decrease in pollen collection, although it may have been beneficial from the standpoint of growth and bloom. The average rainfall during 1954 and 1955 was less than normal during the summer and fall. The most important factor influencing early blooming of shade trees is temperature, and, since the temperature varies from year to year, blooming dates also vary from year to year.

During the latter part of the spring of 1954, the temperature was unusually favorable for bee flight, with the exception of a cold, rainy period covering the last day of April and extending through the first three days of May. This unfavorable weather resulted in no pollen collection for these days. The rainfall at this time was an important factor affecting the summer pollen production.

The years 1954 and 1955 were deficient in rainfall during the summer and fall. During the 1954 summer period rainfall, which occurred during the latter part of May and the early part of June, gave the plants the first good stimulus for growth. Hot weather and a drought during the latter part of June, 1954, affected plant growth and bloom adversely and resulted in a period of extremely low pollen yield (Fig. 3). This unfavorable condition ended with 1 inch of rain July 16 and was followed by a good yield of pollen (Fig. 3). July 15, the quantity of pollen trapped was 21.3 grams. July 18 and 19, the pollen trapped weighed 158.5 grams and 133.25 grams, respectively.

The rainy days during August, 1954, influenced the growth and bloom of the pollen bearing plants and resulted in a good yield of pollen. This favorable period ended with a September drought that caused a decline in pollen collection (Fig. 3).

## SUMMARY

Pollen trapping in the Manhattan, Kansas, area extended from March through October during each of the years 1954 and 1955. Daily collections from pollen traps were weighed; pollen from one of three colonies was sorted according to colors. Pollen grains were examined microscopically for identification. Forty-nine plants were found to be used as pollen sources; 30 of which were identified.

During early spring the major sources of pollen were shade trees, primarily soft maple, elms, boxelder, and redbud. During late spring the major pollen plants were willows, honeysuckle, spiraea, black locust, and honey locust. Dandelions furnished pollen through the two periods. During the summer pasture and field crop plants, including yellow and white sweetclovers, alfalfa, and corn, were the principal sources. During autumn weeds, primarily smartweed and sunflower, were the major pollen sources. Sorghum also yielded large quantities.

Largest collections of pollen were obtained during April, May, August, and September. Pollen collection during spring months is important for increasing the colony population in anticipation of the first major nectarflow. During the autumn months, pollen is important in building the new population that will carry the colony through the winter. Considering the season as a whole, the sources of pollen collected ranked as follows in descending order of magnitude: smartweed, corn, yellow and white sweetclovers, honey locust, sunflower, and soft maple.

Weather factors had a profound influence both on bee activity and plant growth and bloom. Flight activity and pollen collection were largely limited to warm, sunny days. Rainy days hindered flight and, consequently, pollen collection. A rapid rise in temperature in the early spring stimulates certain trees to bloom, thus supplying a source of pollen; at the same time, the elevation in temperature, results in greater field activity of bees in pollen collection. Dry, hot weather and low soil moisture affected plant growth and bloom during late June and the early part of July, 1954, and caused a decrease in pollen yield. Rainfall on July 16 was followed by a good yield of pollen. A similar situation developed during September the same year.

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# Methods of Determining Insecticides in Dead Bees

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## ABSTRACT

*The possible routes by which insecticides, dangerous to bees, may penetrate into the bee body are demonstrated, and the extent of damage caused by such compounds in various European countries is shown. Methods of avoiding such cases are briefly described, namely, the application of compounds safe to bees and the addition of "repellents". Since there have been repeated cases of damage in the past caused by the improper and even prohibited application of insecticides, the necessity of proving the presence of such substances in dead bees is indicated. Hence, methods of determining lethal doses of the various products are of great importance. The quantities of effective substances anticipated and to be determined are of the order of micrograms. In order to reach an international agreement for the determination of insecticides harmful to bees, the section "Bienenschutz" (bee protection) of the IUBS (International Union of Biological Sciences) has begun a library of the methods used in the various countries to detect and identify bee poisoning. The chemical methods for the determination of compounds containing fluorine and arsenic — the representatives of the typical stomach poisons — are briefly described. Separate determinations of substances acting mainly as contact poisons (Parathion, DDT, and Hexachlorcyclohexane) are reviewed. Biological methods for the collective determination of contact poisons are described.*

*The identification of pollen sticking to the hairs on the bodies of poisoned bees establishes the crops being worked prior to death. A study of such crops within flying range may then show what treatment has lead to bee poisoning.*

Damage to bees may occur through the use of pesticides harmful to bees. The possibilities of picking up a poison are as follows:—

- 1) The poison may be taken up together with the nectar, the honey-dew, or the pollen. Further, it may be taken up directly by means of spray drops on the plants or perorally by the residual spray liquid. (Stomach poison).
- 1a) With the nectar a poisonous by-product (systemic insecticide) may be picked up.
- 2) The compound enters the body of the bee by contact with the tarsi or other parts of the body-surface. (Contact poison).
- 3) The use of substances with a high vapour pressure may lead to damages of the bees, when the gaseous insecticide enters the body of the insect. (Respiration poison).

During the years between 1920 and 1930 the fight against pests — especially in orchards — made considerable progress with the introduction of compounds containing arsenic. This progress, however, was accompanied by severe losses of bees. Further losses occurred at that time when wood pests were fought with arsenical compounds on a large scale by aircraft. The situation of the beekeepers became unbearable when during, and especially after, the second world war highly effective, synthetic poisonous substances were used to fight pests. Several countries of northern and central Europe reported severe damages.

In regards to the number of bees killed, the application of contact insecticides when fighting wax-moths was of less importance. Quite considerable, however, are the damages in northern Switzerland, parts of southern Germany and in parts of France caused by industrial gases containing fluorine which affected bees, other animals, and plants.

In improving the organization of the plant protection in fruit growing areas the reports of damages have ceased. The principal losses of bees are now being caused by the treatment of rapefields in bloom, the fighting of the colorado potato beetle (*Leptino-*

*tarsa decemlineata* Say) and the may beetle (*Melolontha vulgaris* L.) as well as weed killing by dinitrocresol.

Naturally, several attempts to reduce the damages done to bees have been made by introducing compounds less harmful on bees. The application of the compound "Toxaphene" which is harmless to bees proved to be quite successful in both ways, i.e. by fighting the pests successfully and by reducing the losses of bees. Further, one has tried to protect the bees from poisoning by adding "repellents" to the highly toxic insecticides. But this had not yet led to any satisfactory success.

In order to avoid unnecessary treatments of plants in bloom — which are still carried out despite all efforts to reduce the damages to bees by the application of insecticides — several countries have issued directives for the protection of bees. If these instructions are violated and losses of bees occur in consequence, legal proceedings may be taken against the violator. In such cases it is, however, necessary to prove that the treatment with chemicals harmful on bees was responsible for the killing. If legal proceedings are taken, the proof of the compound applied is always of the greatest importance. It is, unfortunately rather difficult to conduct such an examination, and sometimes you may even be faced with an unsolvable problem. The toxic values derived from bee tests ( $LD_{50}$  per os)<sup>1</sup> for a few well known compounds give a demonstrative picture regarding the amount of insecticides which are anticipated to be found in the bee body.

Parathion	appr. 0.05	microgram (mcg) per bee
Lindane	" 0.10	"
Dieldrin	" 0.25	"
Aldrin	" 0.3	"
Chlordane	" 1.1	"
Systox	" 1.5	"
DDT	" 8	"
Toxaphene	" 30	"

In practice, the  $LD_{50}$  of the contact poison which is quantitatively even more difficult to determine will — beside the stomach poison — quite frequently lead to bee killings. According to our own tests the toxic effect will be approximately on the same level as that of the stomach poison. The difficulty in determining such small quantities is aggravated by the fact that some of the effective substances are split up in the bee body and others are lost in the lapse of time between the bee killing and the examination.

These statements should have made the problems of the subject on hand sufficiently clear. In order to meet the difficulties on an international basis the section "Bee Protection" of the commission for bee botany of the International Union of Biological Sciences (IUBS) instituted a collection of methods used in the determination of bee poisoning in various countries. The quantities of the toxic substances in the dead bees are in most cases extremely small. It is, therefore, impossible to determine the quantity of poison in a single insect but a considerable number of bees must always be examined to guarantee any certainty of result. When selecting a method of examination one will decide always in favour of the one with the greatest sensitivity and specificity.

#### I. Substances acting as stomach poisons only:

a) Compounds containing fluorine: The dosis letalis for fluorine is approx. 4 to 5 mcg per bee.

1. Determination of fluorine by von Fellenberg (1948). Switzerland. A modified method by Willard and Winter (1933) is used. The fluorine is overdistilled in fractions at a high temperature with the aqueous vapour as hydro-fluorosilicic acid; after neutralization alizarin sulfonic acid is added to the fractions and titrated with thorium nitrate. Determination limit: 10 mcg of fluorine.

<sup>1</sup> $LD_{50}$  = the quantity of poison leading to the death of 50% of the test animals within 24 or 72 hours respectively.



2. Determination of fluorine by Cremer and Völker (1953). Germany (DBR). After treatment with perchloric acid the fluorine is colorimetrically determined by colour diminution of ferrous salicylate complex as hydro-fluorosilicic ( $\text{H}_2\text{SiF}_6$ ) distillate.
- b) Compounds containing arsenic: The dosis details for elementary arsenic is approx. 0.1 mcg per bee. The statements of the different authors vary, however, considerably. The large differences have their origin in the different action of the various arsenic compounds.
  1. Determination of arsenic by Zäch (1945). Switzerland. Twenty-five dead bees are washed and digested with concentrated sulphuric acid and hydrogen peroxyde. Metallic zinc is added and — to achieve an even development of hydrogen — a few drops of copper sulphate solution. The arsenic compounds present are reduced to arsenic hydrogen. The arsenic hydrogen dyes small paper tapes which were soaked in mercuric chloride-solution. The quantity of arsenic contained may be determined by comparison with the gauging scale. Determination limit: 2 mcg of arsenic.
  2. Modified method of determination of arsenic by Sanger & Black (1907). Germany (DBR). The method is similar to that of Zäch (1945), only in the place of mercuric chloride, mercuric bromide is used.
  3. Determination of arsenic by von Fellenberg (1934). Switzerland. Ten grams of dead bees are digested with concentrated sulphuric and nitric acid. After evaporation, distilled water of the same volume is transferred into a little stillhead and is distilled after the addition of concentrated nitric acid, crystallized ferrous sulphate and potassium bromide. Into the distillate hydrogen sulfide is bubbled. From the yellow opalescence which appears at the presence of arsenic one can determine the quantity of arsenic contained by comparison with standards. Determination limit: 2.5 mcg of arsenic.
- II. Separate determinations of materials acting mainly as contact poisons:
  - a) Parathion.
    1. Determination of Parathion by Jachimowicz (1954). Austria. From the Parathion, p-nitrophenol is split off by saponifying with alkali. The alkaline salts of the p-nitrophenol which are coloured intensely yellow serve as a basis for this method. Yellow dye-stuffs present in the bee body must be destroyed by oxydation with hydrogen peroxyde. By means of hydrochloric acid ether the p-nitrophenol released is extracted and sucked up capillarily by small paper tapes. In the course of this process it gathers at the border of the zone of evaporation and becomes visible as a yellow tape after treatment with ammonia. Determination limit: Approx. 10 mcg.
    2. Determination of E 605 by Zeumer and Fischer (1952). Germany (DDR).

The extract of 100 bees is dissolved in a little alcohol. The E 605 present in the solution is reduced to the amino compound by zinc, is then diazolated and coupled with  $\alpha$ -naphthylamine to a pink-violet dye-stuff. This dye-stuff is soluble in chloroform and may be determined colorimetrically. Limit of determination: 10 mcg with a medium error of  $\pm 10\%$ .
  - b) Determination of DDT by Schechter, Soloway, and others (1945). Germany (DDR).

In the bee extract dichlordiphenyltrichlorethane (DDT) is transferred with nitrating acid into tetranitro-dichlordiphenyltrichlorethane which

will combine with sodium methoxide after extraction whence the p,p'-dichlordiphenyltrichlorethane will show a blue colouring. After 15 minutes the blue dye may be colorimetrically determined.

- c) Determination of HCH by Schechter and Hornstein (1952). Germany (DDR).

Hexachlorocyclohexane is dechlorinated to benzene in a special apparatus with zinc in acetic acid. The benzene is nitrated and transferred into m-dinitro-benzene which — after extraction — in the presence of strong alkalis is reacted with methylethylketone. The red-violet dye is measured photometrically. Limit of determination: 5 mcg of Hexachlorocyclohexane.

### III. Collective methods of determining compounds acting mainly as contact poisons

- a) Biological test with *Grillus domesticus* L. by Louveaux (1950). France and Switzerland. The dead bees are deprived of their pollen. This pollen is fed to young specimens of *Grillus domesticus* and the mortality observed. It is the opinion of Louveaux that pollen is the principal means of transporting the poisons. The method is not specific but is effective for both stomach and contact poisons. According to the concentration of the insecticide in the pollen the *Grillus domesticus* is killed as a consequence of external contact or by taking it up orally. With strong doses the contact with the pollen grains is sufficient to cause death; with weaker doses the *Grillus domesticus* must have time to ingest the poison.
- b) Biological test with imagines of *Drosophila melanogaster* Meig. Switzerland. The bees are extracted with chloroform or petroleum ether. The extract is evaporated carefully in a petri-dish. One adds 20 to 30 5-days-old (at most) *Drosophila* to the residue and observes when gyration starts and when death occurs. As a control one puts 20 to 30 *Drosophila* into a petri-dish in which chloroform or petroleum ether has been previously evaporated.
- c) Biological test with *Aedes aegypti* L.-Larvae by Nolan and Wilcoxon (1950). Germany (DBR) and Switzerland. For each test, ten 3-day-old *Aedes aegypti* larvae are placed in a 100 ml cooking beaker with 50 ml. of nutritional solution and observed. The larvae must be nearly of the same size and must show normal vitality. The *Aedes* larvae are extremely sensitive to contact poisons and are killed by trace quantities of these materials. The "signs of poisoning" in the presence of contact poisons show with *Aedes* larvae in that after a few hours their movements become slower, the photostatic reaction is hampered and finally the insects can no longer get to the surface. Determination limit: DDT approx. 5 mcg; Hexachlorocyclohexane approx. 0.5 mcg; E 605 approx. 0.5 mcg.

### IV. Pollen analysis by Lukoschus (1954). Germany (DBR). Fifteen ml of acetone are poured over 50 bees and the rinsing fluid centrifuged. The sediment — according to the instructions by Zander (1935) — will be placed by a loop on object plates and, after the evaporation of the acetone, enclosed in glycerine gelatine at room temperature. In counting under the microscope only the main pollen and the escorting pollen in the sequence of their frequency are evaluated. Single pollen is not taken into consideration, as the complete determination of all plants visited by bees is not important, but only the identification of those principal sources the treatment of which has led to damage to the bees.

The biological tests have proved to be very efficient and simple in application. They possess the great advantage of being highly sensitive but have the disadvantage of non-specificity for various contact poisons. Our experiments to achieve in one process the separation and identification by paper chromatography of the various insecticides has not yet shown any satisfactory result.

These statements are meant to inspire all scientists occupied with these problems to participate in the efforts to institute uniform methods of examination of bee damage as a consequence of the application of insecticides in all countries.

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# Pollen Substitutes

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## ABSTRACT

*Pollen is indispensable for normal development of the honeybee colonies. When pollen is lacking in the spring, beekeepers are offering various pollen substitutes to their bees. A widely used pollen substitute, developed at the Minnesota Agricultural Experiment Station, consists of four parts heated soybean flour and one part dried brewers' yeast by weight. This pollen substitute can be still further improved by an addition of dry skim milk, commercial casein, and dried egg yolk.*

Pollen is essential for the growth and development of bees. Very often in the spring there is not enough natural pollen present in the hives to provide for a vigorous development of honeybee colonies. In this case, giving a good pollen substitute or pollen supplement is desirable. On the basis of work done at the Minnesota Agricultural Experiment Station (Haydak, 1945), a pollen substitute consisting of four parts soybean flour (expeller processed or heated, fat content 5-7 percent) and one part dried brewers' yeast by weight was recommended.

In order to find out the comparative value of pollen, pollen supplement, and pollen substitute, a series of experiments was undertaken at the Minnesota Agricultural Experiment Station. Experimental colonies of approximately the same strength, consisting of bees not over 10 hours old, were placed in isolated screen cages into nuclei containing three pollen-free combs. A fertile, good-laying queen was introduced to each colony. For the first seven days the food was supplied in the form of a honey paste smeared into the cells of the combs; later a candy made by mixing honey and the material tested was given. Sugar solution and water were offered ad libitum. After the first sealed cell was observed the open and sealed brood was counted three or four times at 10-day intervals. The indices of food efficiency were obtained by assigning one point to the food producing the lowest count of sealed brood cells, and dividing the averages of sealed brood cells count in the colonies supplied with other foods by this lowest average. The results of the experiments are presented in the following tables.

From Table I it is evident that pollen substitutes containing soybean flour and dried brewers' yeast, alone or fortified with dried egg yolk, were superior to pollen supplement in which one year old pollen from pollen traps was used.

From Table II it appears that beebread was vastly superior to pollen substitute not fortified with dried egg yolk. Addition of 10 percent pollen (from pollen trap, one year old) to the substitute increased the nutritive value of the diet.

Since the protein content of the pollen substitute paste was only 6 percent and that of the candy only about 12 percent, while pollen collected by bees, on an average, contained close to 20 percent, it was decided to increase the protein content of the pollen substitute by an addition of finely ground commercial casein. The results are presented in Table III.

Table III shows that a simple addition of skim milk solids considerably improved the diet. An increase in the protein content of the diet gave still better results. Two year old pollen (from pollen trap) had an inferior nutritive value. This confirms the findings of Maurizio (1954) who showed that even one year old air-dried pollen loses its nutritive value considerably.

According to deGroot (1953), Maurizio (1954) and Wahl (1954), none of the pollen substitutes tried by them was equal to good pollen. Consequently, in 1956 a comparative test between pollen substitutes and pollen collected by the bees at the time of the experiment, was attempted. Two colonies were used in testing each diet. Because, at the third count a diseased condition of larvae in the colonies fed commercial casein supplement appeared and nosema infection was found in the pollen-fed colonies, the average results of the counts for the first two 10-day periods only are given in

<sup>1</sup>Paper No. 3643, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.



TABLE I — Comparison of Pollen Substitute and Pollen Supplement (1944).

Supplement to Soybean flour	Strength of Colonies gm.	Dead bees gm.	Mortality per cent	Brood rearing									
				I Period			II Period			III Period			Total No. sealed brood cells No.
				Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Brood production index No.	
DSM*	1660	458	27.5	2334	95	116	1317	106	678	2556		1.0	
(4:1)													
Pollen	1645	488	29.6	1559	315	516	954	399	135	2474		1.0	
(4:1)													
DBY	1686	523	31.0	2011	595	1485	1431	1383	260	4879		2.0	
(9:1)													
DBY + DEY	1654	464	28.1	3017	1161	1015	2401	1325	897	5357		2.2	
(9:1:1½)													

\*DSM, dried skim milk; DBY, dried brewer's yeast; DEY, dried egg yolk; SBF, soybean flour; CC, commercial casein.

TABLE II — Comparison of Pollen Substitute and Beebread (1952).

Diet	Strength of Colony gm.	Dead bees gm.	Mortality per cent	Protein in the diet						Brood rearing									
				Paste	Candy	I Period			II Period			III Period			Total No. sealed brood cells No.	Brood production index No.			
						Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.					
SBF:DBY*	1702	328	19.3	7.0	14.0	954	346	430	447	598	301	1982		1.0					
(3:1)																			
SBF:DBY	1739	293	17.0	7.0	13.9	2204	357	592	948	774	298	3470		1.8					
(3:1)																			
+ 10% Pollen																			
Beebread	1700	237	14.0	2.7	20.0	8502	1890	2518	3064	6831	3521	17851		9.0					
in combs																			

\*For explanation of symbols see Table I.

Diet	Strength of Colony gm.	Protein in the diet		Brood rearing												Total No. sealed brood cells No.	Brood production index No.		
		Dead bees gm.	Mortality per cent	Paste per cent	Candy per cent	I Period			II Period			III period			IV Period				
						Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.			Sealed cells No.	Unsealed larvae No.
SBF:DBY:DEY*																			
(3½:1:1½)	765	129	16.9	7.4	15.5	1489	228	386	404	545	228	337	182	2557	1.0				
SBF:DBY:DSM:DEY																			
(2½:1:1:1½)	771	149	19.3	6.4	13.9	2395	890	685	530	658	365	813	187	4551	1.8				
SBF:CC:DBY:DSM:DEY																			
(1:1½:1:1:1½)	777	125	16.1	8.3	22.1	3408	1173	1223	1124	414	1393	619	768	5664	2.1				
CC:DBY:DSM:DEY																			
(2½:1:1:1½)	790	124	15.7	9.9	30.9	2811	851	1054	474	570	962	1725	419	6160	2.3				
Pollen	779	192	24.6	2.9	12.4	278	229	60	219	72	115	—	—	410	—				

\*For explanation of symbols see Table I.

TABLE IV — Comparison of Pollen and Pollen Substitutes (1956).

Diet	Strength of Colony gm.	Dead bees gm.	Mortality per cent	Protein in the diet		Brood rearing						Total No. sealed brood cells No.	Brood production index No.
				Paste per cent	Candy per cent	I Period			II Period				
						Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.	Sealed cells No.	Unsealed larvae No.		
SBF:DBY:DSM:DEY*	1493	145	9.7	6.3	12.5	4942	1633	3986	6236	1.0			
(2½:1:1:½)													
SBF:CC:DBY:DSM:DEY	1481	109	7.3	8.5	21.2	7295	2345	2591	10154	1.6			
(1:1½:1:1:½)													
CC:DBY:DSM:DEY	1502	147	9.8	9.9	28.1	6580	1688	2038	8090	1.3			
(2½:1:1:½)													
Pollen	1477	136	9.2	5.0	12.7	7933	2046	4214	9365	1.5			

\*For explanation of symbols see Table I.

Table IV. Since in the previous year's experiment the colonies fed these diets continued to rear brood normally during four 10-day periods, nutritional deficiency in the commercial casein supplemented colonies could probably be ruled out. Moreover, in deficiency cases, nurse bees usually eat the larvae, so nothing is left in the cells. No cannibalism, so characteristic for deficiency, was observed. Also, in deficiency, all larvae would be affected, so there would be no adult bees produced. In the present case there were 100-200 sealed cells in each affected colony and adult bees were emerging during the third and fourth consecutive 10-day periods. These facts would further support the contention that no nutritional deficiency was involved. Microscopical examination of the dead larvae did not show the presence of any pathogenic bacteria. This phenomenon will be investigated further.

From Table IV it is evident that when, in order to increase its protein content, pollen substitute is supplemented with commercial casein, the nutritive value of such diets as were used in the experiment was about equal to the pollen used simultaneously by the colonies in the apiary. The food was consumed well in all cases. However, the consumption of pollen was more than twice that of the pollen substitutes.

Under the conditions of the experiment, the nutritive value of pollen substitutes fortified with protein in the form of commercial caseins was not inferior to that of pollen collected by the bees at the time of experiment. The nutritive value of pure pollen diminishes with age.

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# Royal Jelly — Its Collection and its Therapeutic Role

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## ABSTRACT

Of late royal jelly has taken on, in France, some therapeutical importance (intramuscular injections). In 1955 over 200 kilograms were collected. The quality of the product may be determined by physical tests among which the measurement of conductivity is especially interesting and enables one to easily detect any addition of honey; the examination of the drug is completed by a microscopic study; the colour of the jelly in alkaline solution, the determination of the number and size of the exuviae enables one to determine whether the jelly was collected within the prescribed dates and with the necessary care. On the other hand, the pollens present in the jelly give information on its origin and collection date.

Bees accept, in the hive, capsules made of various materials (glass, plastic material, mineral wax) and deposit royal jelly therein. There is in the hive a certain substance incorporated in the waxes that arrests the building of cells. It is likely identical to Butler's royal substance and Pain's ecto-hormone, but there is also another substance antagonizing the former one which would also be incorporated in the waxes.

Royal jelly injected in rabbits brings about a temporary neutropenia and a lasting reticulocytosis; along with a breakdown of ascorbic acid in the adrenal glands. On mice or rats, the action on growth is light or null, the action on the gonads is very inconstant; shortly after the injection the disappearance of the phosphatases in the cortico-adrenal gland is noted in association with a lowering of hepatic glycogen and of muscular glycogen. This apparently is a stress that, however, exercises no adverse action on the organism.

In humans, after intramuscular injections, neutropenia and reticulocytosis are equally noted along with a modification in the elimination of the 17-ketosteroids. All these conditions are accompanied by a very characteristic euphoria with a renewal of strength and appetite; the action may be prolonged several weeks, there is no inurement.





# Preference of Honeybees for Sugar Solutions

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## ABSTRACT

*The attractiveness to honeybees of different concentrations and combinations of sucrose, fructose and glucose were investigated under controlled conditions. The results of these studies indicate that bees are able to distinguish differences of 5 per cent in concentration. Significantly more bees were attracted to a 50 per cent solution than to dishes containing 45 per cent and 40 per cent sucrose solutions. When the difference in concentration was narrowed from 5 per cent to 2.5 per cent the bees were unable to distinguish between solutions containing 50, 47.5, and 45 per cent sucrose.*

*There was no difference in bee activity on dishes where the ratio of fructose to glucose was varied but the sucrose and total solids content were held constant.*

The apparent variation in the foraging activity of honeybees on plants which bloom during the same period has stimulated research in nectar secretion. Several investigators, including Vansell (1934) and Butler (1945) found that the attractiveness of a nectar depended upon its volume and concentration. von Frisch (1934) showed that solutions of sucrose, fructose, and glucose, the normal constituents of nectar, were readily accepted by honeybees. Wykes (1952) determined the attractiveness of equal volumes of sugar solutions varying in composition but of the same total concentration. She found that the different sugars were not equally attractive to honeybees. Preference for solutions of single sugars were in the following descending order; sucrose, glucose, maltose, and fructose. The data of Wykes do not show that honeybees exhibit a greater preference for solutions of sucrose, fructose and glucose as compared to the single sugar, sucrose.

The experiments of Kunze (1933) and von Frisch (1934) on the responses of bees towards various sugar solutions were designed primarily to establish threshold values and their data do not agree. A series of experiments were carried out to determine whether honeybees could discriminate between sucrose solutions of varying concentration and between solutions consisting of the three sugars, sucrose, glucose and fructose.

## MATERIALS AND METHODS

All experiments were conducted within a screened enclosure, the dimensions of which were 20'  $\times$  12'  $\times$  8'. The dishes used were designed so as to expose a constant volume of syrup throughout the experimental feeding period. Small cans, with a capacity of approximately 300 ml, were perforated near the lip and inverted on metal lids of slightly larger diameter. The bees were able to feed without difficulty on the exposed syrup. A rectangular table, 3'  $\times$  6', painted with white enamel, was used to hold the dishes. All solutions were prepared on a weight basis and expressed in percentage concentration.

Several five-frame nuclei were used for the feeding trials but only one nucleus was placed in the screen house at one time. A training period was necessary to direct the bees of each nucleus to gather syrup from the dishes prior to the commencement of a series of feeding tests. Four solutions, replicated seven times, were used in each test where sucrose solutions were varied as to concentration. Only three solutions of mixed sugars were used and these were replicated eight times. The table containing the sugar solutions was placed in the house for an interval of approximately one-half hour before counts were recorded. The number of bees feeding on each dish was counted at ten-minute intervals during a two-hour period.

It became evident from preliminary tests that certain dishes on the table were almost completely ignored by the bees irrespective of the concentration of the syrup therein. In order to cope with this situation it was considered essential to establish a bee-activity factor due to dish-position. Consequently, a group of 24 dishes, each containing the same concentration (40 per cent), were placed on the table in an irregular

pattern but with the position of each identified. Counts were recorded of the number of bees visiting each dish at ten-minute intervals during a two-hour period. This procedure was repeated for three successive days and an average value obtained. The activity or correction factor was obtained by dividing the number counted on all dishes into the total number of bees counted on any one dish. The reciprocal of this value was then assigned as the factor for that dish. When the sucrose solutions and the mixed sugar solutions were exposed in the house for experimentation the number of bees counted on each dish was multiplied by the activity factor for that dish. The concentration of sucrose offered ranged from 20 per cent to 55 per cent. In the experiments with sugar mixtures only one concentration was used.

## RESULTS

### SUCROSE SOLUTIONS

The total number of bee visits to dishes containing sucrose solutions of 30 to 50 per cent concentration, in increments of 10 per cent, are summarized for two separate experiments in Table I. These data show a significant difference between the means, thus indicating that the bees could distinguish between these concentrations.

TABLE I. Visitation Rate on Sucrose Solutions with 10 per cent Variations in Concentration.

Expt. No.	20%	30%	40%	50%
A1. Total (14 counts)	67	217	367	1012
Mean	9.4	31	52.4	144.5
L.S.D. ( $P = .05$ ) 9.52				
A2. Total (14 counts)	137	294	521	754
Mean	19	42	74	107
L.S.D. ( $P = .05$ ) 17.9				

In Tables II and III the increments between concentration of the sucrose solutions were reduced to 5 per cent and 2.5 per cent respectively. It will be observed from the data shown in Table II that there were significantly more bees visiting dishes with the higher concentrations. With the differences in concentration limited to 2.5 per cent (Table III) the bees were unable to distinguish between concentrations of this order.

TABLE II. Visitation Rate on Sucrose Solutions with 5 per cent Variation in Concentration.

Expt. No.	40%	45%	50%	55%
B1. Total (14 counts)	308	511	713	1052
Mean	44	73	102	149
L.S.D. ( $P = .05$ ) 27.5				
	30%	35%	40%	45%
B2. Total (13 counts)	57	206	458	1373
Mean	8.1	29.4	65.4	196.1
L.S.D. ( $P = .05$ ) 11.7				

The data summarized in Table IV were recorded while conducting observations on the behaviour of scout bees on the feeding dishes. A significantly greater volume of sucrose solution was removed from dishes with a 50 per cent concentration than those containing 40 per cent and the latter solution was more acceptable than the 30 per cent solution. These data corroborate the visitation rates presented in Table I.

TABLE III. Visitation Rate on Sucrose Solutions with 2.5 per cent Variation in Concentration

Expt. No.	47.5%	50%	52.5%	55%
C1. Total (14 counts)	490	504	817	758
Mean	70	72	116.7	108.2
L.S.D. (P = .05) 28.6				
C2. Total (14 counts)	522	461	693	614
Mean	74.3	65.8	99	87.7
L.S.D. (P = .05) 16.04				

TABLE IV. Amount of Sucrose Solutions of Different Concentration Removed by Bees.

	30%	40%	50%
Total (ml.)	181	260	403
Mean (4 replicates)	45	65	101
L.S.D. (P = .05) 15.9			

## MIXED SUGAR SOLUTIONS

The experiments concerned with the mixed sugar solutions of the same concentration are presented in Table V. It will be noted that on three separate trials the bees did not exhibit a preference for one solution over another.

TABLE V. Visitation Rate of Bees on Syrups of Different Constituents

Composition of Syrup (40%)			First Trial (Means)	Second Trial (Means)	Third Trial (Means)
S:	G:	F*:			
4	1	1	408	448	239
4	0	2	459	501	273
4	2	0	422	521	224

\* S = Sucrose, G = Glucose, F = Fructose

## GENERAL OBSERVATIONS ON BEHAVIOUR OF SCOUT BEES

Some general observations were made on the bees that approached the dishes shortly after the feed was placed in the screened house. A few of these bees were painted and their behaviour was observed when they returned to a glass observation hive. The dances performed by these bees appeared as the figure of eight lying in a horizontal position. The pattern of the dance resembled that described by Tschumi (1950) who has referred to a "Sicheltanz", sickle or crescent dance, when the food source is more than 10 meters but less than 100 meters from the hive. The distance of the food source from the hive during these observations was approximately three meters. No wagging movements were performed by the bees observed during their figure-of-eight patterns.

## GENERAL DISCUSSION

While it is recognized that the behaviour of the bees under the conditions of the experiments reported herein might differ from that which would occur in an unconfined area, nevertheless, the bees were always offered several different concentrations of sucrose and in the experiment with mixed sugars several choices were also offered. These results show that honeybees can distinguish between sucrose concentrations vary-

ing by 5 per cent as indicated by the significantly higher population on dishes with the highest sugar content. They could not, however, distinguish between solutions that were varied by 2.5 per cent but corroborated the earlier results by showing a higher population on the dishes differing by 5 per cent.

The results with solutions consisting of sucrose, fructose and glucose; sucrose and fructose; and sucrose and glucose did not show that bees could distinguish between these sugars at a concentration of 40 per cent. It was considered likely that the sucrose-fructose solution might be more attractive to bees than the sucrose-glucose mixture but this was not evident. According to von Frisch (1934) different sugars have only the one quality of taste stimulus, that of sweetness to the honeybee.

If the sugar concentration of nectar is the only factor in determining its attractiveness to the honeybee one would expect a higher population visiting the flowers of plants secreting the highest concentration, providing the quantity of nectar is not limiting.

#### ACKNOWLEDGEMENTS

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# The Use of Fluorescent Markers as an Aid in Studying the Foraging Behaviour of Honeybees

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## ABSTRACT

Fluorescent materials used to mark honeybees for subsequent identification offer an advantage in that they can be positively identified, even when present in minute quantities, by passing the sample insects under an ultra-violet light. In the form of powders, these materials can readily be applied to bees — either at the entrance of the hive, or to individual foragers. Certain markers, when applied in excess to honeybees, or to blossoms, will be carried and distributed by foraging bees, so that visited blossoms can be detected by surveying the area at night with a portable ultra-violet light.

Field data collected through the use of this technique indicate that:

1. Honeybees from colonies newly moved into an area tend to concentrate their initial foraging activities in the vicinity of their colony location, and may forage under less favourable weather conditions than will bees from previously established colonies.
2. Honeybee foragers marked in the field tend to return to the same foraging area. The degree of fixation to a given foraging area was more pronounced on legumes than on tree fruits.
3. Honeybees used for the pollination of spring-blooming tree fruits show a tendency to drift with the wind from the colony to the orchard. Later in the season on legume crops this tendency is reversed.
4. Honeybees can effectually transport pollen from entrance inserts to tree fruit blossoms.
5. Bumblebees do not have as limited a foraging area as do honeybees.





# The Foraging Behavior of Honeybees on Hairy Vetch

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## ABSTRACT<sup>1</sup>

The alternate methods bees can use in foraging from blossoms of hairy vetch are described. The process of learning the foraging method, some environmental factors which affect the proportions of different types of foragers, and a postulate to account for the environmental influences are presented. Data are also presented on changes in the proportions of bees gathering different forage, the foraging area, the foraging speed, the reactions of bees to competing foragers, the distance between successive racemes visited by bees, and individual differences between foragers. The environmental influences, particularly the nectar flow, which influences these aspects of behavior are discussed. Differences in the behavior of bees foraging from hairy vetch blossoms and from blossoms of several other legumes are presented briefly.

<sup>1</sup>This paper was published in *Insectes Sociaux* 3: 537-549 (1956); 4: 43-57 (1957).



# Organization and Operation of a Bee Breeding Program

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## ABSTRACT

*The most important single operational factor in the smooth conduction of a bee breeding program is proper scheduling of activities. The extent of the program is limited by the number of test and line maintenance colonies which can be utilized; and the rapidity with which those colonies are established is governed by the number which can be established per week and the number of queens which can be inseminated per week.*

*The above considerations form a general outline of the yearly program. The outline is amplified by a decision as to the number of breeding queens to be used and the number of daughters to be included in each family group. It is further expanded by an estimate of the number of cells needed to produce each group of queens, and the number of drones needed to supply mates for the queens.*

*The scheduling of the various operational activities rests upon drone maturity dates. A special form is described which is used to lay out the program and to co-ordinate the various operations.*

*The classification of colonies used, the composition and care of the service colonies, the technique and instruments of artificial insemination employed, and the records and filing systems are described.*

The organization and yearly operation of a bee breeding program can be divided into five distinct parts: (1) scheduling the work, (2) production of inseminated queens, (3) testing, (4) genetic analyses and selection of next generation mothers, and (5) distribution of stock to ultimate users. In this discussion we will omit item 4, genetic analyses and selection of next generation mothers, and touch on item 3, testing, and item 5, distribution of stock to ultimate users, only briefly.

## SCHEDULING THE WORK

The importance of carefully scheduling the work cannot be overemphasized. A few queens from each of many different lines must be reared and mated in a short period of time, and the synchronization of proper mating age of the queens with that of the drones so the work load is evened out requires precise planning and meticulous execution of the work scheduled.

### DRONE EMERGENCE DATE

The drone maturity dates, or better, the drone emergence dates, are the pillars upon which the entire schedule rests. Drones can be expected to live for twenty days following emergence. Some die much sooner and others live much longer, but a large proportion will be in excellent condition when twenty days old. The first eight to ten days after emergence constitute a period during which drones attain sexual maturity, and this is followed by a ten to twelve day period of reliable usefulness for mating.

It should be mentioned that it is perfectly possible to leave drone combs in the breeding hives for long periods so drones emerge frequently in the hives. When this practice is followed partial drone combs should be used. Queens may lay very well in partial drone combs when they will not lay in full ones. By marking the drones, or confining them to the breeder hives by large and deep entrance excluders, mature drones from the breeders are generally available. This system certainly has some advantages, especially when certain drones are needed over an extended period, and it does not require such careful planning. It also has some very definite disadvantages which can easily outweigh the simplified planning. One of the most serious disadvantages is the destruction of the drone brood by the bees, which frequently occurs when the weather changes from bright and warm to cold and rainy. This is especially likely to occur when full drone combs are used. We have found that a more positive control over the rearing of drones is preferable for our locality.

### QUEEN IDENTITY NUMBERS

Queens and their mates must be identified in some way, but in the initial stages of planning the year's work neither the queens to be mated nor their mates exist. We are thus faced with a problem of identification of the participants to the mating. Since drones are genetically gametes of their mothers, the mating between a queen and a drone is genetically a mating between a queen and the mother of the drone. Thus, with certain reservations, the drone may be ignored in the pedigrees and the male side of a mating can be specified by naming the drone's mother. Each inseminated queen, on the other hand, must be individually identified, as must each mating, but it is convenient to identify a group of sisters by their mother's number. Therefore we identify a mating by specifying the mother of the queen and the mother of the drone, although identifications can be made in a general way by using line designations and referring to matings within or between lines, such as B x T.

We actually use four kinds of numbers. Each queen selected to be a breeder queen is given a number which designates her line and her sequence in the breeding structure of that line. The line designations are carried through the female side only, that is, from mother to daughter and never from mother to son. Only breeding queens have breeding numbers, and these specifically identify queen and drone mothers.

Every queen which heads a colony also has a specific and permanent number which identifies her but does not indicate her lineage. This number is derived from the nucleus or hive number where the queen first heads a colony, the year, and the sequence of the queen in the nucleus or hive. For instance N 144-563 means the queen was the third one in nucleus 144 in 1956.

Queens emerged in cages and introduced to nuclei or colonies after insemination have no hive or nucleus number initially and thus no permanent identity number. It has been found convenient to designate each group of caged sister queens by the mother's breeder number or nucleus number, and each daughter queen by a sequence number. Thus B 16-4 would identify the fourth daughter of breeder B 16 to be inseminated from a cage in any given year. The use of this mating number is purely transitory and the number is no longer used after the queen is placed in a colony, although it remains permanently in the mating book.

The fourth type of number is used to identify breeding queens sent to cooperators. These numbers are prefaced by UCD (University of California, Davis), and are permanent. A queen's UCD number is her place in the sequence of UCD numbers.

### USE OF SCHEDULE (MATINGS) FORM

*Listing and matings to be made:* The synchronization of mating age of queens and drones and the maintaining of an even work load becomes complicated when many different kinds of matings are to be made in a short space of time. We have found it most helpful to use a special schedule sheet for this, called the "Matings" form (Fig. 8).

Assuming that the breeding queens have been selected, the first step in scheduling the work is listing the breeders and matings to be made in "Stocks and Matings" section of "Matings" form. The queen mothers are listed in the "Virgin's mother" sub-section of this form, and the drone mothers in the "Drone's mother" sub-section. The drone mothers are paired with the virgin mothers to specify with which drones the virgins will be mated.

The numbers of sister queens to be included in each mating group are decided upon and these figures entered in the upper left corner of the proper spaces of the "Virgin mating" sub-section. The numbers of bars of cells needed to produce the required number of virgins of each group are entered in the upper left hand corner of the proper spaces of the "Graft" column of the "Virgins" section, and the numbers of cages of drones needed for each mating are entered in the upper left hand corner of the proper spaces in "Cage drones" column of the "Drones" section.

This listing constitutes a statement of what is to be accomplished. The next step is to schedule the operations involved in the production of inseminated queens.

*Drone production schedule:* A decision must be made on the number of queens which will be inseminated per week. Upon the basis of this, drone combs are put into



enough drone mother colonies each week to produce the required drones. The date the combs are given the breeders is entered in the "Comb in breeder" column of the schedule. If virgins from several queen mothers are to be inseminated from one drone emergence from a particular drone mother, one mating is chosen as the main one (usually the mother-daughter mating) and the "Comb in breeder" dates of the other or subsidiary matings are enclosed in parentheses. The "Comb in feeder" and "Cage drone brood" dates may be omitted from the subsidiary matings. Other drone emergences from a drone mother already used establish new "Comb in breeder" dates for that drone breeder.

The drone combs usually remain in the breeding colonies five days, after which they are transferred to feeding colonies. When the drone combs with eggs and larvae are transferred to the feeding colonies they are marked with the breeder number and the date. This date together with the feeder colony number, is entered in the appropriate "Comb in feeder" space of the schedule. The drone emergence dates for each comb are calculated and entered in the "Drone emergence" column. From the drone emergence date the "Drone maturity" date and the "Cage drone" date are calculated and entered in their appropriate spaces of the schedule. Performance of an operation is indicated by a check mark beside the date.

*Virgin production schedule:* It is convenient to graft on Tuesdays and Fridays. Tuesday grafts come out of the cell builder on Friday ten days later, and Friday grafts come out on Mondays. The Monday or Friday which comes nearest to preceding the drone maturity date by five to eight days is chosen as the "Cells out" date for each mating. From this date the remaining operation dates including the insemination date are calculated and entered in their respective places in the schedule for each group of sister queens of each mating. A tally is kept of cells committed (to be grafted) to prevent overload.

## PRODUCTION OF INSEMINATED QUEENS

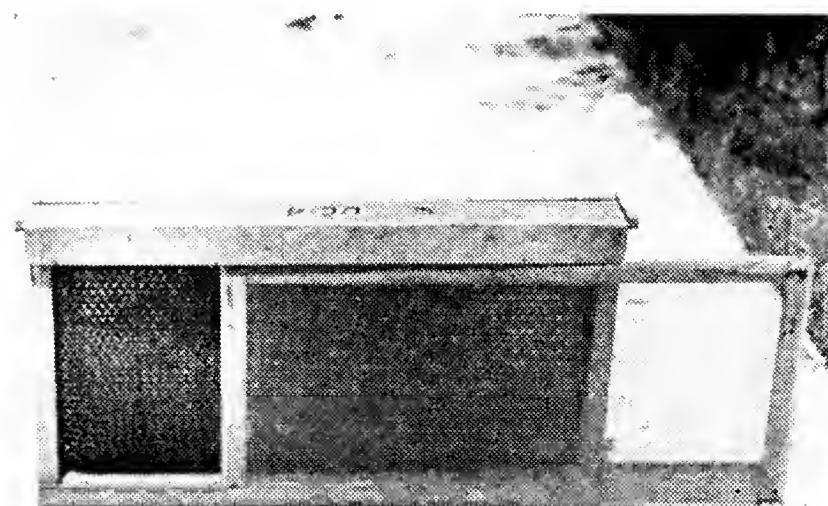
For convenience, the colonies used in the breeding program are divided into four groups: (1) breeding colonies, (2) service colonies, (3) testing colonies, and (4) field colonies. The service colonies are classified further as: (1) feeding colonies, (2) cell building colonies, (3) nursery colonies, and (4) supporting colonies.

### COMPOSITION AND MAINTENANCE OF SERVICE COLONIES

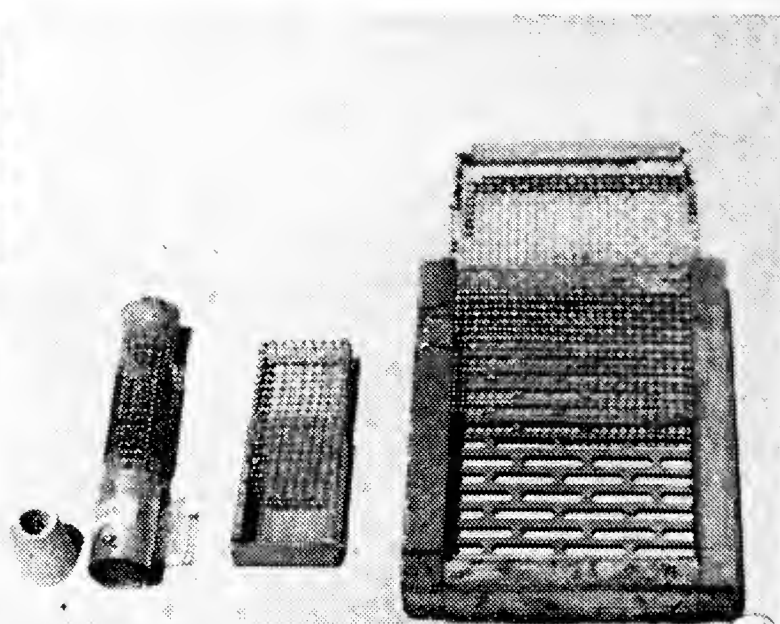
*Feeding colonies:* The feeding colonies are used to rear drones and to feed grafting larvae prior to grafting. They are queenless and may be one, two, or three stories high. These colonies are made up with a frame of honey and pollen next to each sidewall and the remainder of the space is filled with sealed brood. Package bees are added to make them very strong and they are fed continuously with sugar syrup and pollen or supplement and yeast. As larvae are placed in the colony the combs from which bees have emerged are removed and replaced by the frames of larvae. Package bees are added each week to keep the population strong with young bees.

*Cell building colonies:* The cell building colonies are queenless and one or two stories high. A frame of honey and pollen is placed next to each sidewall of the body in which the cells are built. A frame of pollen is put in the second position from the right. The newest graft occupies the third position, a frame of young larvae the fourth, and the next youngest graft is the fifth. The oldest graft occupies the sixth position and the remaining spaces are filled with frames of honey and pollen. Package bees are added to make the colony very strong. The colony is supplied with sugar syrup and pollen, or supplement and brewers yeast continuously, and before each graft a new frame of larvae is put in the fourth position and package bees are added. These colonies start and finish the cells.

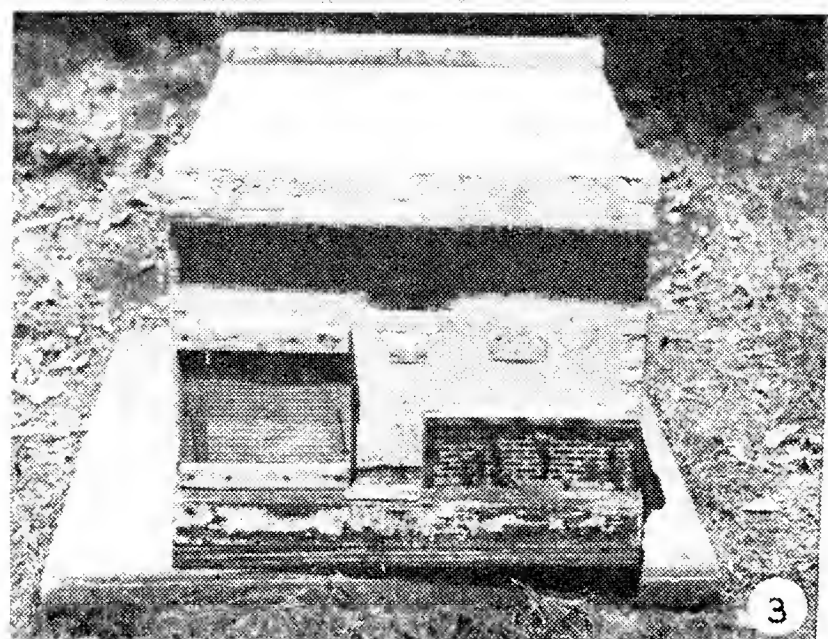
*Nursery colonies:* Nursery colonies are used to emerge cells and care for virgin queens, to mature and care for drones, and to care for caged inseminated queens. Separate nursery colonies are maintained for virgins, drones, and inseminated queens. They are queenless and one or two stories high. Each body contains nine frames which are arranged so there is a frame of honey and pollen next to each sidewall and one in the center. A frame of larvae occupies the third position from each side. This arrangement leaves four spaces for frames of caged queens or drones, one space on each side



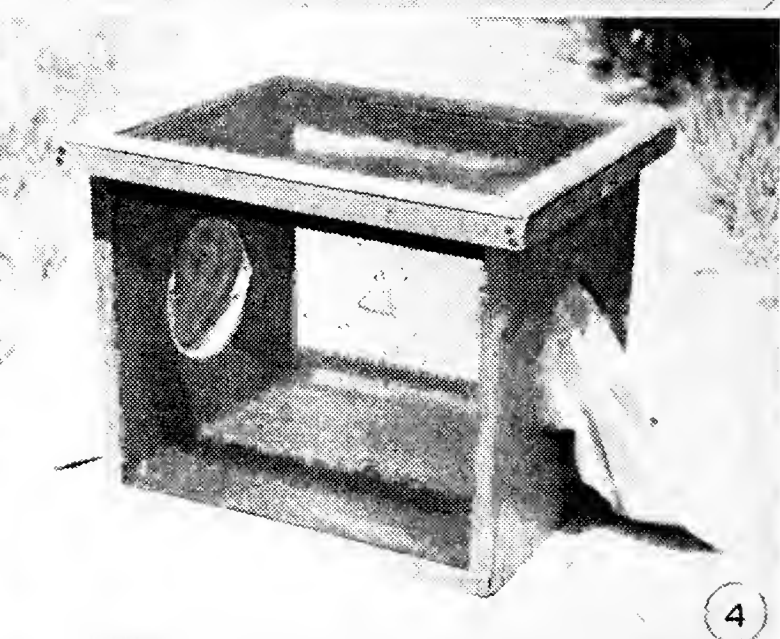
1



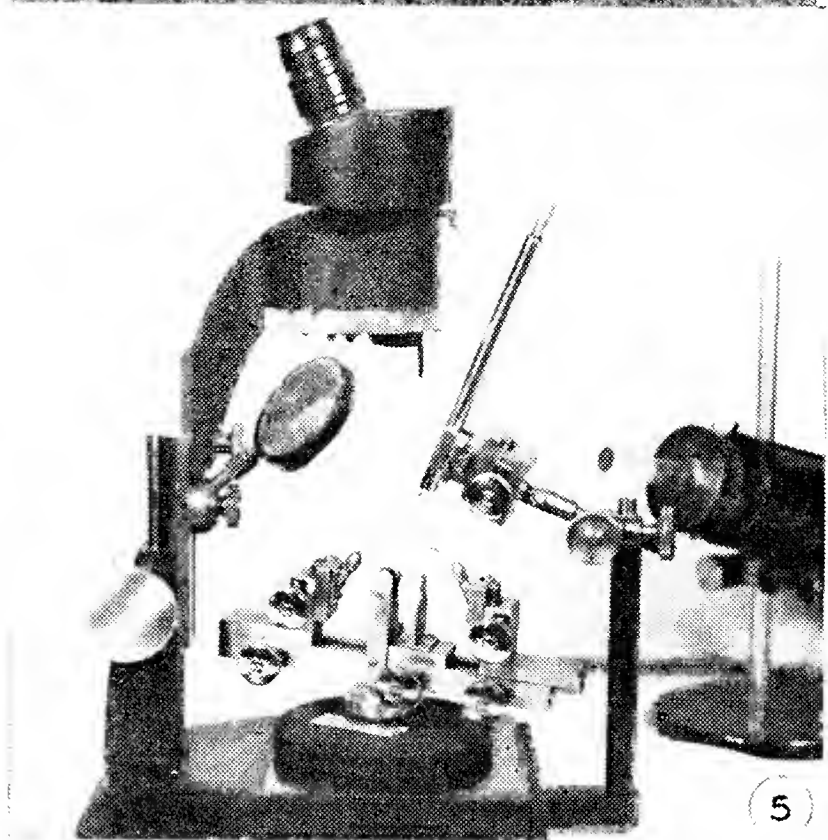
2



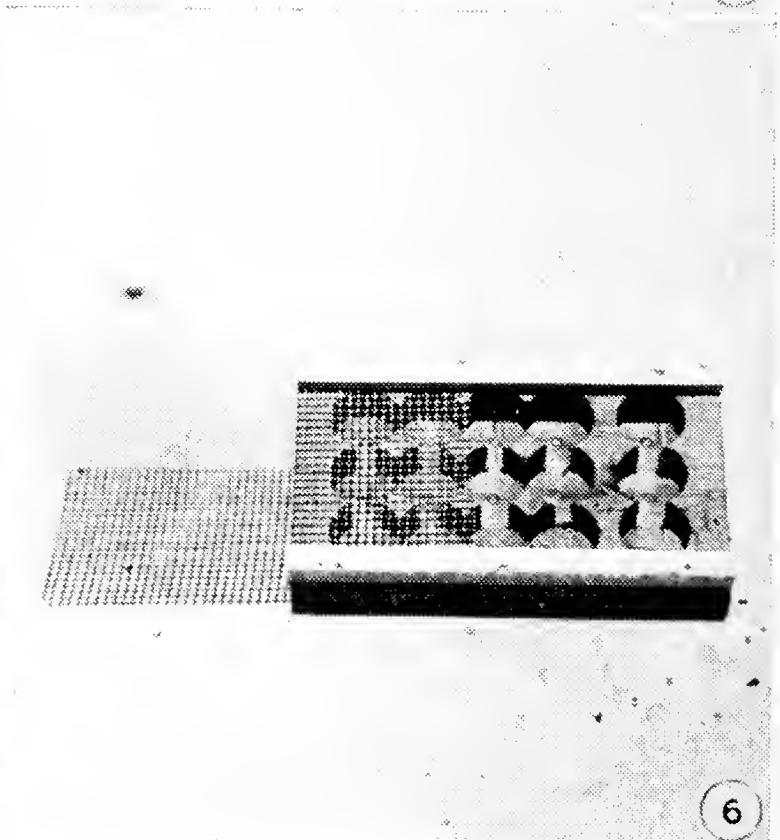
3



4



5



6

Fig. 1. Special comb cage.

Fig. 2. Inseminated queen, virgin, and drone maturing cages.

Fig. 3. Entrance excluder and robber screen.

Fig. 4. Drone flight box.

Fig. 5. Insemination instruments.

Fig. 6. Virgin-drone shipping cage.

of each frame of larvae. Package bees are added to make the colony very strong. These colonies are fed continuously with sugar syrup and pollen or supplement. New larvae and package bees are added once a week.

PRODUCTION OF DRONES

The breeding colonies are strengthened in the early spring by the addition of sealed brood, or, after caging the queen, by the addition of package bees. The space occupied by the cluster may be reduced by a follower board. Drone combs which have been warmed and polished over support colonies are placed in the first group of breeders. About five days later these are marked with the breeder number and the date, and are transferred to feeding colonies. The identifying marks are covered with scotch tape to prevent the bees from removing them. All identifying marks exposed to the bees must be covered with scotch tape.

Two days before emergence the frames of drone brood are caged in special comb cages, Fig. 1, and are put into an incubator which is maintained at 92°F. and is humidified with a pan of water.

On the day of emergence, or the day following, the drones are caged in maturing cages, Fig. 2, and are put into nursery colonies where they remain until used or discarded. They are ready for use eight to ten days later and usually survive well and in good condition for ten to fifteen days after reaching maturity. The schedule is checked as these operations are performed, and the caged drones are listed on a drone locator sheet which has the following headings:

Drone locator					
Date caged	Colony	Frame	No. cages	Stock	Remarks

The drone entries in the locator are lined out as the drones are used or discarded.

PRODUCTION OF VIRGINS

A warm and polished comb is placed in the broodnests of the breeder colonies five days prior to grafting. Two days later these combs are marked and transferred to feeder colonies. On the day of grafting, the larvae are the right age and are floating on a bed of jelly which covers the cell bottom in a thick layer. In grafting, much of the jelly is transferred with the larvae. Either single or double grafts are used.

Cells are distributed to nuclei or are caged, Fig. 2, in nursery colonies on the tenth day following grafting. Nuclei entrances are covered by excluder, Fig. 3. The schedule is checked and the locations of the virgins are listed on a virgin locator sheet which has the following headings:

Virgin locator						
Date cells out	Breeder	In nuclei	In cages			Remarks
			No. cells caged	Hive	Frame	

Virgins emerged in nuclei are clipped two days later and are given a ten minute CO<sub>2</sub> treatment. Those emerged in cages are left unclipped in the cages until inseminated, but they also are given a ten minute CO<sub>2</sub> treatment when they are two or three days old. In some cases queens are emerged in the cages in the nursery and are then placed, still caged, in nuclei they are to head. They are released upon insemination. Occasionally virgins are emerged in cages in a nursery colony, and certain selected ones are dropped into nuclei while they are still very young, or if older, they may be introduced from a cage. In either case an excluder is tacked over the entrance.

The nuclei are housed in one story ten-frame hives. The entrance is half closed and is provided with a robbing screen, Fig. 3. The robbing screen is adjusted to the need for protection. During periods when robbing is easily started the entrance excluders are fitted with hardware cloth to cover all of the excluder except a small corner entrance.

Cells placed in nuclei are recorded in the current year's "Yard book". The yard book is a bound notebook perpendicularly ruled to take the entries of two or three nuclei on a page. This book constitutes a permanent record of the queens which have occupied each nucleus during the year. As the queens are removed or the nucleus



otherwise becomes queenless a line is drawn under the entry. These entries form the bases for the individual queen numbers.

### INSEMINATION

All queens used to establish lines and to propagate lines, and all mothers of hybrid queens must be artificially inseminated. The technique employed is described below.

The virgins are caught from the nuclei or they are taken from the virgin nursery colony, and a cage of the proper drones is obtained from a drone nursery. In the laboratory the cage of drones is put into the drone flight box, Fig. 4, and a few drones are released. A fruit grading lamp, standardized to 5500°K, is suspended above the flight box to make the drones fly, because active drones evert the copulatory organ and ejaculate the semen better than sluggish ones.

The queen manipulator, Fig. 5, is placed to the left side of the microscope. The queen is anaesthetized and is then held by the abdomen between the thumb and the forefinger of the left hand while her thorax is inserted into the anaesthetization chamber of the queen manipulator. She should be oriented midway between the sides of the chamber with her venter toward the operator. She is clamped in this position between the sponge rubber facings of the chamber and the movable closing piece. The carbon dioxide gas flow should be adjusted to a small stream. The queen is left thus while the syringe is filled.

The syringe is prepared by filling the end of the barrel with distilled water or physiological salt solution containing an antibiotic, or sulfathiazole, and the syringe tip is screwed into place. Part of the water or solution is then forced from the tip by turning the syringe screw, and the discharge of solution is stopped when the fluid plunger will withdraw to the threads at the base of the tip when the screw is reversed. The fluid is again forced down the tip to within 3 mm of the end. The syringe is now ready for use and it is clamped in the syringe manipulator, Fig. 5.

A drone is selected and the thorax crushed between the thumb and middle finger. If this does not initiate eversion the abdomen is squeezed with quick but moderate pressure (do not mash) between the thumb and forefinger until the copulatory organ appears at the end (or the abdomen is compressed by pushing the terminal segments inward until the penis appears), and the pressure is immediately released. If the abdomen contracts, ejaculation has probably occurred. If it remains flaccid, ejaculation probably did not take place. As the abdomen begins to contract, moderate pressure may again be applied and held until eversion and ejaculation are completed or after the initial eversion stops the eversion may be completed by a quick and forceful pressure on the contracted abdomen and the penis base. By this method the semen is frequently separated from the mucus. However too much pressure may cause the penis to rupture with consequent loss of the seminal fluids. It should be emphasized that absolutely no fecal matter should be taken into the syringe and the semen should not be permitted to touch the drone's abdomen, wings or legs. Any contamination may result in the death of the queen. Five cubic millimeters or more of semen are taken into the syringe if the queen is to be inseminated once and three millimeters or more if the queen is to be inseminated two or more times. After the semen is taken from each drone it is withdrawn into the syringe tip one millimeter from the end to prevent its drying. Some of the translucent mucus or watery bulb fluid may also be taken up but none of the white mucus which will coagulate in the syringe and plug the median oviduct and probably the syringe. After the syringe is filled it is raised as far as the manipulator will take it.

The queen manipulator with the queen is now brought to the microscope stage. The sting chamber is opened with fine forceps inserted into the sting chamber between the sting shaft and the sternum and while holding the sting chamber open the sting shaft is pressed anteriorly which turns the sting base to a better position for placing the sting hook. The dorsal sting hook is brought over the queen past the sting and is lowered to the anterior sting chamber wall. It is then moved dorsally and is fitted between the bases of the sting lancets. (The queen can be moved with the forceps in any direction on a horizontal plane to aid in fitting the sting hook.) The ventral hook is now brought over the queen and into the sting chamber and the forceps are withdrawn.

The ventral hook is adjusted and then the dorsal hook so the sting is pulled from over the vaginal orifice and the anterior sting chamber wall is flat but is stretched very little.

The syringe is now lowered into the sting chamber and the queen manipulator is moved over the microscope stage until the end of the syringe tip is over or just dorsal to a brown spot ventral to the vaginal orifice. The syringe is then raised a little and the vaginal probe is inserted into the vagina Fig. 7, A. The ventral vaginal lip is pulled open and the probe is pushed toward the sting until it goes beyond the end of the valvefold, B. It is then slipped under the valvefold, C, and the valvefold is pulled posteriorly and ventrally, which leaves the vagina wide open and the orifice of the median oviduct exposed, D. The valvefold is held firmly in this position while the syringe is inserted into the vagina, E. Care must be taken not to catch the syringe on the orifice edge. The probe is now removed and the syringe tip pressed firmly against the reproductive opening until the surrounding tissues move with the syringe, F.

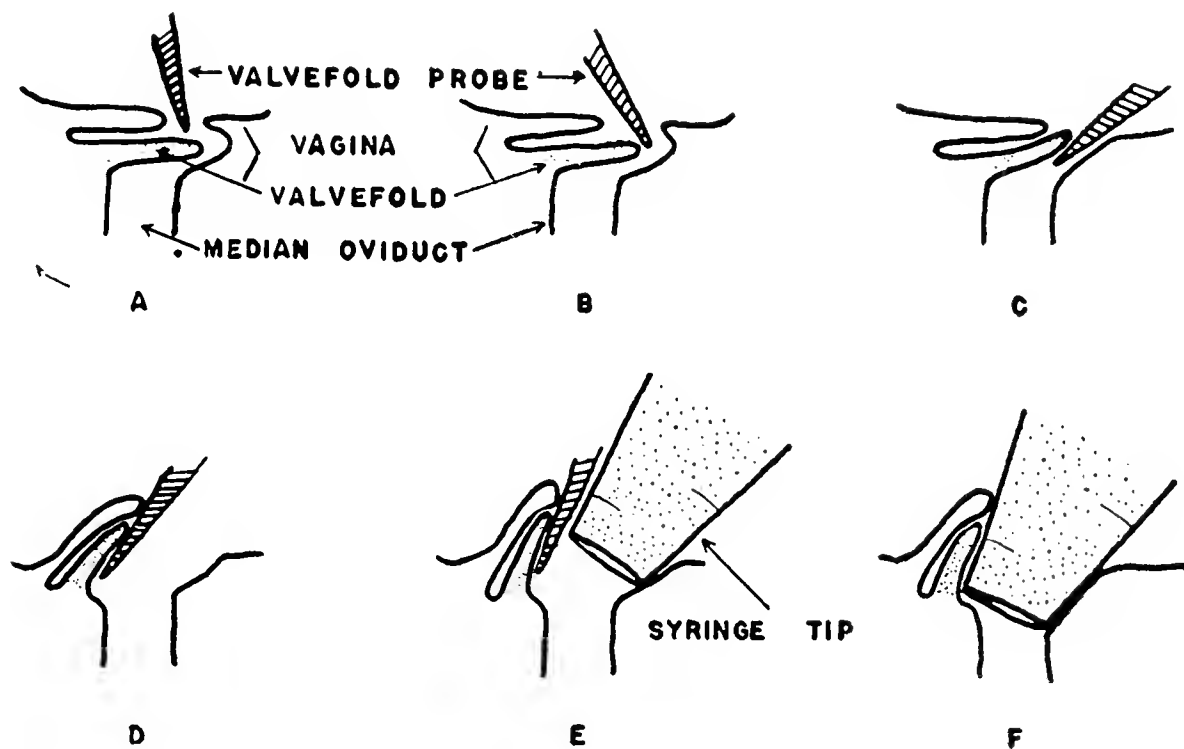


Fig. 7. Insertion of syringe.

The position of the syringe is tested by a slight turning of the syringe screw. If semen moves easily down the syringe the tip is correctly placed. If not, the syringe is improperly placed or semen has dried in the syringe tip and the cause of the trouble should be ascertained and remedied. The semen is injected and the syringe raised. The fluid plunger is run to the end of the tip to prevent semen from drying on the inner tip walls.

The hooks are disengaged and moved up and away from the queen. The queen is removed from the anaesthetization chamber and the distal end of the unclipped wing is cut off to indicate the queen is inseminated. A record is made in the insemination record book (mating book) or on the breeding or genetic record form. The insemination record book is a bound notebook, and the different kinds of matings (or the same matings made on different dates) are listed on separate pages. It forms a permanent record and is especially useful when queens are inseminated from cages. A page has the following arrangement of the entries.

#### INSEMINATION RECORD

Date      N # x N #; Queen mother breeder # x Drone mother breeder #  
 Nucleus #      Queen mother # — sequence #  
 (of insem.  
 queen)

The nucleus numbers in the date column refer to nuclei in which the queens were emerged or into which they were introduced. The identity numbers to the right of the date column consist of the queen mother number and virgin sequence numbers and are used only for queens caged in nurseries. These identity numbers are transitory and are not used after the queen is introduced to a nucleus or hive, the number of which is then entered in the date column opposite the queen concerned.





The queen is returned to the nucleus. If she had been loose in the nucleus she is released on the face of a comb or, if still anaesthetized, is dropped between the combs. If she had been caged in the nucleus since emergence and is inseminated once she is given a carbon dioxide treatment the day before insemination and is released following insemination.

If the queen was emerged in a nursery she is transferred to an insemination cage Fig. 3, and is put in the inseminated queen nursery. After insemination and carbon dioxide treatments are finished the solid cork of the cage is replaced with one having a  $\frac{5}{16}$  inch hole filled with queen cage candy, and the cage is placed horizontally between combs in the center of the cluster of her new colony. The nucleus must be fed, and an excluder must cover the entrance until the queen lays.

The schedule and queen and drone locators are checked to show that the queens have been inseminated and the drones used.

Breeding queens to be sent to cooperators are inseminated from cages in the nursery colonies. When the cooperator receives an inseminated queen, he prepares a package of bees from several colonies and suspends the queen in her cage in the package. The package and queen are allowed to sit in a cool place for three days after which the package is installed. In this case also it is imperative that an excluder be placed over the entrance until the queen lays and that the new colony be fed.

Occasionally queen breeders desire to have certain crosses made from their own bees. The queens and drones may be shipped in either of two ways. In some cases the beekeeper will ship the queens in 2-hole cages in a package, with the drones loose among the bees of the package. In other cases the queens and drones are shipped in special virgin-drone cages with the queen and her escorts in a regular 3-hole compartment, one hole of which is filled with candy, and the drones and their escorts are in a 9-hole compartment, two holes of which are filled with candy, Fig. 6.

### TESTING

A full discussion of testing would consume far more time than we have available, but no matter how testing is done one of the essential features is a description of each colony. The description consists of observations taken throughout the test period and the observations should be recorded in such a way the data are readily available for analysis. We use a form for this purpose, the Breeding Record, which has a section at the top for identification and other unchanging notations, and a columnar list of observations or manipulations. A series of parallel columns provides spaces for recording the observations and each of these columns is headed by a space for the date the observations were taken. The observations are recorded in terms of rating numbers, 1 to 5, wherever possible, with 1 being the poorest and 5 the best. In some cases other measures are used; population for instance is recorded in terms of frames. No allowance for adverse conditions are made at the time the observations are taken but a note is appended mentioning the conditions so they may be considered when the queens are evaluated. The Breeding Record remains in the office and a yard sheet based on the Breeding Record is taken to the field. The following explanation of ratings gives in detail the ratings used in describing a queen and her colony.

Explanation of ratings for "characters" listed on Breeding Record form (Fig. 9) are as follows:

1. **Population** = Strength of colony in frames of bees.
2. **Propolizing** = Amount of propolis deposited on frames and bottom board.  
5 = practically none. 4 = slight amount. 3 = usual amount. 2 = quite noticeably more than usual.  
1 = masses of propolis sticking to frames and bottom board.
3. **Temper** = Tendency of bees to sting.  
5 = very gentle, bees remain on combs, very seldom sting, do not fly to face, do not fly around head, do not fly or jump at fingers, practically no smoke needed. 4 = gentle, bees remain on combs, need occasional smoke, seldom sting. 3 = touchy, bees fly at fingers, fly from comb to face, require smoke 2-3 times per body. 2 = cross, bees fly around head, fly at fingers, fly at face, sting arms, require smoke each frame. 1 = very cross, bees fight clothes, sting arms, fly around head, fight veil, sting viciously, follow around apiary, require nearly constant smoke.
4. **Quietness on comb**  
5 = lie flat and very quiet on combs. 4 = quiet on combs, not flat, move about freely. 3 = nervous, move about jerkily. 2 = bees run over combs in groups. 1 = very nervous, run off combs, or hang in bunches.
5. **Brood**
  - a. **amount** — Total amount of brood in terms of frames. (Full frame has brood occupying all cell area).
  - b. **solidness** — appearance of brood — solid or spotty.  
5 = 0-3 empty cells/100 cells sealed brood. 4 = 4-7 empty cells/100 cells sealed brood. 3 = 8-11 empty cells/100 cells sealed brood. 2 = 12-20 empty cells/100 cells sealed brood. 1 = over 20 empty cells/100 cells sealed brood. (Same for eggs, but indicate **eggs**).

- c. **reach** — Extent queen extends egg laying toward comb edges.  
5 = 0 rows empty cells between brood and lower comb edge or stores; overlay bees. 4 = 1 row empty cells. 3 = 2 rows empty cells. 2 = 3 rows empty cells. 1 = over 3 rows empty cells.
  - d. **gradation** — Brood becomes progressively younger from a central point toward the edges — as just sealing at the center and eggs at the outside.  
5 = brood same age at center, evenly smaller toward edges. 4 = brood for most part same age at center and smaller toward edges — some scattering. 3 = brood of same age tends to be at center, mixed with brood of other ages, considerable scattering. 2 = . 1 = brood of same age scattered over comb and mixed with brood of all ages, no definite center.
  - e. **viability** — Mortality of eggs and/or larvae, pupae, or adults before emergence. (actual percentage).
  - f. **rate** — Average number eggs laid per day in test period.
  - g. **arrangement**  
5 = compact broodnest. Brood together regardless of amount of room and strength of colony. All brood combs well filled before queen lays in others. 4 = Brood together for most part. 3 = some partially filled combs. 2 = Considerable scattering of brood. Many partially filled combs. 1 = Most combs partially filled. Brood excessively scattered.
  6. **Disease resistance** = Susceptibility to disease (Afb, Efb, sac, nosema, paralysis)  
5 = no disease. 4 = light, very few cells or bees. 3 = moderate. 2 = heavy. 1 = very heavy.
  7. **Pollen arrangement**  
5 = toward sides, and between brood and honey, very few cells among brood. 4 = toward sides, and between brood and honey, small amount among brood. 3 = . 2 = considerable pollen among brood. 1 = solid combs among brood.
  8. **Industry** = Gathering of stores. (nectar and pollen).  
5 = storing heavily. 4 = storing moderately. 3 = storing lightly. 2 = maintaining. 1 = using stores.
  9. **Wax working** = Drawing foundation (or building comb).  
5 = drawing foundation rapidly. 4 = drawing foundation moderately rapidly, and evenly. 3 = drawing foundation slowly, and evenly. 2 = drawing foundation very slowly, and/or unevenly. 1 = neglect foundation.
  10. **Enter supers** = Willingness to occupy added super of combs.  
5 = occupy supers readily. 4 = . 3 = occupy supers slowly. 2 = . 1 = occupy supers not at all, or very slowly.
  11. **Swarming**  
5 = do not swarm even when crowded. 4 = swarm when crowded, but respond to manipulation and room. 3 = swarm when crowded, do not respond to added room and manipulation. 2 = swarm before crowded. 1 = swarm when weak.
  12. **Supersedure** = Replacement of queen by one reared naturally in colony.  
5 = over 24 months. 4 = 12-24 months. 3 = 6-12 months. 2 = 3-6 months. 1 = less than 3 months.
  13. **Longevity** = Length of life from emergence. (actual age in days)
  14. **Flight** = Early and late, and in adverse weather. (actual time or temperature flight begins and ends).
  15. **Robbing tendency**  
5 = Do not rob even when very adverse conditions; nor (5a) are robbed themselves. 4 = Rob under very adverse conditions; or (4a) are robbed themselves only when greatly overwhelmed. 3 = Rob when no flow; or (3a) are robbed with difficulty. 2 = Rob in light flow; or (2a) are robbed fairly easily. 1 = Rob in heavy flow (almost always try to rob); or (1a) do not defend colony.
  16. **Wintering**  
5 = Come through winter strong and with heavy stores. 4 = Come through winter moderately strong and with moderate to heavy stores. 3 = Come through winter moderately strong to strong and with light stores. 2 = Come through winter weak with moderate to heavy stores. 1 = Come through winter weak with light stores. 0 = Did not survive winter.
  17. **Honey production**  
Enter here for proper date the number of frames of honey removed or added (basis of full frame). Or actual pounds removed or added.  
**Net honey produced** = difference between honey present on first examination or at makeup plus honey given (including comparable value of syrup fed) and honey removed plus honey remaining. Also calculate for test period.  
**Honey per bee (frame)** = Increase in honey in hive divided by number of bees (both in terms of frames for estimate) in definite test period.
  18. **Pollen production**  
Enter here the pollen removed or added in terms of frames, or actual amount trapped, or square inches removed, or actual amount added.  
**Net pollen produced** = as for honey.  
**Pollen per bee** = as for honey.
  19. **Brood added or removed**  
Frames of brood added or removed. (Basis of full frame).
  20. **Bees added or removed**  
Frames of bees added or removed. (Basis of full frame).
  21. **Combs added or removed**  
Empty combs or nearly so.
  22. **Foundation added or removed**  
Number of frames.
  23. **Honey stores**  
Frames of honey.
  24. **Pollen stores**  
Frames of pollen.
- Superscripts: + = top of class  
— = bottom of class.

Judge worker characteristics and colony characteristics only after colony consists of queen's workers.

The Genetic Record form is used to record all data pertaining to the study of mutants or other traits not lending themselves to the list of characters in the Breeding Record.

#### FILING

The Breeding Records are folded outwardly at the center and filed alphabetically and numerically in 5x8 inch file drawers. An index of breeder queen numbers for each stock is kept on "number" sheets just behind the main index guide of each stock. The breeder queen numbers of the stock are listed in numerical sequence (the number

**Nucleus:** \_\_\_\_\_

Laying: \_\_\_\_\_ Type: \_\_\_\_\_ Queen: \_\_\_\_\_ Mate: \_\_\_\_\_ Progeny: \_\_\_\_\_  
Inbreeding: \_\_\_\_\_ Queen: \_\_\_\_\_ Drone Mother: \_\_\_\_\_ Relationship: \_\_\_\_\_ Bees: \_\_\_\_\_

CHARACTER
COLONY POPULATION
PROPOLIZING
TEMPER
QUIETNESS ON COMBS
BROOD:
amount
: solidness
: reach
: gradation
: viability
: rate
: arrangement
DISEASE:
afb
: efb
: sac
: paralysis
: nasema
:
POLLEN ARRANGEMENT
INDUSTRY:
nectar
: pollen
WAX WORKING
ENTER SUPERS
SWARMING
SUPERSEDURE
LONGEVITY:
worker
: drone
FLIGHT:
time
: temperature
ROBBING TENDENCY
WINTERING
HONEY PRODUCTION
POLLEN PRODUCTION
BROOD + or -
BEEES + or -
COMBS + or -
FOUNDATION + or -
HONEY STORES
POLLEN STORES

Fig. 9. Breeding record.

Genetic records are also folded outwardly at the middle and are filed numerically by colony number in 5x8 file drawers. Mutants are indexed on number forms which are filed alphabetically, a number sheet for each mutant. However, the numbers on the mutant index are colony numbers, and the genetic formulae are shown in the spaces to the right of the numbers. Where more than one mutant is involved in a queen and her mate each mutant is listed on the appropriate index.

Estimates in terms of frames are based on completely filled or covered frames and are expressed as wholes and decimals.

It should be mentioned that cooperators, through necessity, test the queens strictly on a rough estimate and comparative basis. However, each cooperator receives a "standard" line and one of the "test" lines each year and comparisons are made between these as well as with other stock. The cooperators are encouraged to use the standard line daughters to requeen their bees near their queen yards. When this is done selected mates are provided in abundance for the following year and queens of all cooperators mate with the same stock to a large degree.

#### DISTRIBUTION

Distribution of breeding queens is made by the California Bee Breeders Association. The University furnishes the Association with inbred lines which the Association propagates. Crosses are made between designated lines to produce mothers of 2-line hybrid queens. These mothers are purchased by the queen breeders and are used one year only. At the close of the active season practically all of the queen breeder's colonies are requeened with daughters of the current breeders. These daughters will become the drone mothers the following year. Each summer, also, new breeders are purchased for use in the next season. The worker bees consequently will be 4-line hybrids. By controlled rotation of crosses the quality of hybrid bees is maintained.



# Comparative Value of Different Pollens in the Nutrition of *Osmia lignaria* Say<sup>1, 2</sup>

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## ABSTRACT

A technique was devised for collecting completed nests of *O. lignaria* and transferring the eggs from the natural pollen balls to experimental diets made up of a number of pure species of pollens collected by honey bees.

Aside from the natural diet, pollen from waterleaf (*Hydrophyllum capitatum*), only pollen from pea (*Pisum sativum*), mustard (*Brassica nigra*), and alfalfa (*Medicago sativa*) allowed complete development of the larvae to the adult stage. Pollen from gumweed (*Grindelia squarrosa*), greasewood (*Sarcobatus vermiculatus*), povertyweed (*Iva axillaria*), and dandelion (*Taraxacum officinalis*) was not sufficiently nutritious to allow complete development. The adults from larvae reared on honey bee collected pollens were all smaller and developed slower than larvae feeding on the natural diet, waterleaf.

Greasewood pollen supplemented with vitamin-free casein increased in nutritive value but not enough to permit development to the adult stage. Yeast added to casein-supplemented greasewood pollen improved it enough to allow complete development. Further addition of dried egg yolk to greasewood pollen containing casein and yeast further increased the growth rate. This improvement indicates the deficiency in greasewood pollen of some or all of the B vitamins found in yeast and of cholesterol found in egg yolk. It also shows the need of *O. lignaria* for these dietary components.

Formulations of artificial diets have also been offered to *O. lignaria* but so far none have allowed any significant growth. Prospects for developing a favorable artificial diet appear to be favorable.

All nonparasitic bees have the instinct to store honey and pollen. Nectar supplies bees with the carbohydrate portion of their diet. Pollen is a rich source of all the other materials needed for their growth.

In spite of the importance of pollen in the nutrition of such a large group of beneficial insects, there is much yet to be known about it. Only recently analyses by Todd and Bretherick (1942), Vivino and Palmer (1944) and others have separated some of the nutritional components of various species of pollens. Several investigators have fed pollens and pollen substitutes to adult honey bees (*Apis mellifera* L.) and evaluated the diets by such criteria as adult longevity (DeGroot 1952, 1953) and pharyngeal-gland, ovarian, and fat-body development (Soudek 1929, Maurizio 1954). Other workers have fed test diets to adult bees and measured the amount of brood reared. Haydak (1933, 1949), Haydak and Tanquary (1943), and Schaefer and Farrar (1941) reported considerable progress in developing practical pollen substitutes and determining some of the nutritional requirements of honey bees.

The ideal way to study the nutritional needs of honey bees and the relative values of pollens and substitute diets is to feed them directly to the larvae. This has not been done successfully because honey bee larvae require a special diet prepared by adult nurse bees. So far this diet has not been synthesized by man, although Michael and

<sup>1</sup> Hymenoptera-Apoidea

<sup>2</sup> Also published in *Bee World* 38(9):221-226, 1957.

Abramovitz (1955) succeeded in rearing 3-day-old larvae to adulthood on a substitute diet.

This paper describes a method for comparing the nutritive value of different pollens by feeding them directly to larvae of a solitary bee, *Osmia lignaria* Say.

### MATERIALS AND METHODS

Eggs of *Osmia lignaria* were obtained from several locations in the hills surrounding Cache Valley, Utah. Shady, forested areas, where waterleaf (*Hydrophyllum capitatum* Dougl.) was abundant, were found to have high populations of female bees. This species normally places a linear series of brood cells in beetle burrows in logs, stumps, and branches close to the ground. It was found that they could be induced to nest in artificial burrows consisting of a split round wooden stick drilled with a  $\frac{3}{8}$ -inch bit to a depth of 5 inches, when they were placed where female bees could find them.<sup>3</sup> When the nest series was completed, it was taken to the laboratory and opened. The egg was removed from the natural pollen ball and transferred to a small vial containing the experimental diet. *Osmia*-collected pollen from the completed nests was used for making up control diets. The vials were kept in a constant-temperature cabinet maintained at 80° F. and a relative humidity of 50-60 percent.

The pollens tested were obtained from pollen traps placed on the hive entrances of honey bee colonies. The pellets were air-dried and then ground to a fine powder in a Wiley mill. When these powders were placed in the temperature cabinet for 48 hours, they absorbed enough moisture to attain the approximate consistency of natural *Osmia*-collected pollen. The pollens used, together with their protein and nitrogen contents, are given in Table I.

TABLE I. Pollens Fed to Larvae of *Osmia lignaria*.

Pollen	Percent Nitrogen*	Protein (N × 6.25)
Waterleaf ( <i>Hydrophyllum capitatum</i> Dougl.)	3.8	23.7
Mustard ( <i>Brassica nigra</i> L.)	3.6	22.5
Alfalfa ( <i>Medicago sativa</i> L.)	3.6	22.5
Greasewood ( <i>Sarcobatus vermiculatus</i> Hook.)	2.2	13.7
Gumweed ( <i>Grindelia squarrosa</i> (Pursh) Dunal)	2.6	16.2
Povertyweed ( <i>Iva axillaris</i> Pursh)	1.7	10.6
Mixture of five pollens	2.8	17.5
Balsam root ( <i>Balsamorhiza sagitata</i> (Pursh) Nutt.)	2.5	15.4
Pea ( <i>Pisum sativum</i> L.)	3.7	23.4
Dandelion ( <i>Taraxacum officinalis</i> Web.)	2.4	15.1

\* Percent of fresh weight.

The growing larvae were weighed daily, or at less frequent intervals. The amount of food consumed and the duration of the feeding stage were also noted. Adults which developed were weighed and analyzed for protein content. From these data the relative value of the diets was determined.

<sup>3</sup>Levin, M. D., 1957. Artificial nesting burrows for *Osmia lignaria* Say. Jour. Econ. Ent. 50: 506-507. 1957.

## RESULTS

The experiments were conducted during three seasons. The preliminary work in 1953 showed that waterleaf pollen, the natural diet, permitted the fastest growth and produced the largest bees. Mustard pollen and the mixture of pollens were second best, followed by alfalfa pollen. Larvae grew larger but more slowly on the last pollen. Larvae fed gumweed, greasewood, and povertyweed pollen never developed far past the second molt, and those fed povertyweed pollen developed the least. The duration of the feeding period was inversely proportional to the peak weight of the larvae, a relationship confirmed in subsequent seasons.

Of the ten diets tested in 1954, only five permitted development to the adult stage. Again the natural diet of waterleaf pollen allowed the maximum growth in the shortest time, as shown in Table 2. Pea pollen was next. The other pollens were distinctly lower in nutritive value, and differences between them were not marked. Gumweed pollen, either pure or supplemented, did not allow development past the early third instar. The addition of vitamin-free casein to this pollen increased larval longevity from 11 to 21.4 days, although there was little more actual growth. The separate addition of cholesterol and yeast to gumweed pollen increased larval longevity to 13.2 and 12.8 days, respectively.

Twelve diets, some of which were supplemented pollens, were tested in 1955. Development was completed on only seven. As in previous tests, gumweed and greasewood pollens were unsatisfactory. Dandelion allowed considerably more growth, but none of the larvae feeding on it matured. The addition of 13 percent of casein appeared to improve greasewood pollen (diet S-2) much more than it did gumweed pollen, but not enough to allow complete development. When diet S-2 was further supplemented with 4.2 percent of yeast (diet S-3), three out of five larvae became adults. Four out of five larvae completed their development when fed diet S-4, which included 0.9 percent of egg yolk as well as casein and yeast.

TABLE II. Nutritional Value of Different Pollens  
for *Osmia lignaria*, 1954 and 1955.

Pollen	Peak larval weight (milligrams)	Feeding period (days)
1954 Tests		
Alfalfa	94.7	23.5
Black mustard	69.6	27.4
Pea	109.8	19.7
Waterleaf	175.8	14.6
Mixed	68.0	25.0
1955 Tests		
Waterleaf		
New	237.5	13.0
Old	187.0	14.8
S-5	176.7	15.0
Alfalfa		
New	103.8	18.2
Old	103.4	21.2
Greasewood		
S-3	47.7	24.0
S-4	55.5	21.0

Waterleaf pollen gave the best growth response again in 1955 (Table II) and the addition of 2.2 percent of vitamin-free casein (diet S-5) appeared to have little effect. A decrease in nutritive value appeared to be associated with increased age of the pollen. Greasewood pollen supplemented with casein plus yeast (S-3) allowed complete development, but the adults were much smaller than those reared on waterleaf and alfalfa pollen. Further increase in growth response resulted from the addition of egg yolk (diet S-4).

TABLE III. Protein Efficiency of Several Pollen Diets Fed to Larvae of *Osmia lignaria*, 1955.

Diet	Protein content (%)	P.E. Ratio		
		First 7 days	After 7 days	Entire feeding period
Waterleaf:				
New	19.3	2.8	2.7	2.7
1-year-old	20.4	3.1	2.2	2.6
S-5	21.9	3.2	1.3	2.1
Alfalfa:				
New	21.6	2.8	1.9	2.4
1-year-old	22.4	2.1	1.8	1.9
Greasewood:				
S-3	20.2	2.4	1.5	1.7
S-4	19.9	2.0	2.1	2.0

TABLE IV. Nutritional Value of Several Pollen Diets as Indicated by Weight and Nitrogen Content of Adult *Osmia lignaria*, 1955.

Pollen diet	Fresh weight of bees* (milligrams)	Dry weight of bees		Nitrogen consumed	
		Percent of fresh weight	Percent nitrogen	Total* (milligrams)	Percent retained
Waterleaf:					
New	142.3 (6)	46.9	7.7	13.1 (3)	37.2
Old	118.8 (6)	56.8	8.6	11.7 (4)	45.3
S-5	104.6 (4)	46.4	8.0	12.9 (3)	35.4
Alfalfa:					
New	49.0 (7)	67.9	9.0	7.2 (4)	40.7
Old	66.5 (4)	49.8	10.3	9.0 (3)	39.3
Greasewood:					
S-3	30.5 (3)	48.2	13.5	4.4 (2)	46.0
S-4	36.9 (2)	46.1	14.0	4.4 (2)	54.1

\* Figures in parentheses indicate number of adults included in weight.

Protein Efficiency (P.E.), the gain in weight/protein consumed, was calculated for the first 7 feeding days, for the feeding period after the first 7 days, and for the entire feeding stage, as shown in Table III. The natural waterleaf-pollen diet had the highest P.E. ratio, especially during the first part of the feeding period. The P.E. ratio decreased in all diets during the later stages of growth. Weight and nitrogen data obtained from the adults are presented in Table IV. Waterleaf pollen produced the heaviest adults with the lowest nitrogen content. Nitrogen retention, the biological value of the protein, improved sharply when egg yolk was added to the diet composed of greasewood pollen, casein, and yeast (diet S-4).

GENERAL DISCUSSION

Waterleaf pollen, the natural food of *Osmia lignaria*, was the best diet tested. In every test larvae on this diet ate the most food, grew the fastest, reached the highest peak weight, and developed into the largest adults.

Pea pollen was the only honey bee-collected pollen in 1953 that approached waterleaf pollen in nutritive value. Alfalfa, mustard, and the mixture of pollens were fairly uniform in this respect, but they were all inferior to waterleaf and pea pollens.

The pollens allowing complete larval development had more than 17 percent of protein, and those poor in nutritive value had less than 17 percent. In 1954, adding vitamin-free casein to gumweed and greasewood pollen increased the protein level and resulted in a slightly better growth response. However, none of the larvae fed on such supplemented pollens reached adulthood. This shows that the protein level alone was not responsible for the inability of *Osmia* larvae to reach the adult stage. The improvement in growth following the addition of yeast and egg yolk (diets S-3 and S-4) to the casein-supplemented greasewood pollen (diet S-2) furnishes further evidence that other factors besides protein level are involved. When thus fully supplemented, greasewood pollen had all that the larvae required for complete development. Apparently this pollen lacks some or all of the B vitamins found in yeast, and also cholesterol, which is required by insects (Fraenkel & Blewett 1943) and is abundant in egg yolk. These dietary factors appear to be essential to the growth of *Osmia* larvae.

Since even the supplemented diets were not as good as the natural one, it appears that the supplementary materials were not added in optimum proportions. A similar imbalance of essential dietary factors probably accounts for the lower nutritive value of those honey bee-collected pollens that permitted complete development. It is possible, too, that the waterleaf pollen contained an additive substance derived from the nest-making adult *Osmia*.

The 1955 work suggests that aging can have a detrimental effect on the nutritive value of pollens. However, the evidence is not conclusive, since the pollens were not collected from the same location both years. The possible effect of different climatic conditions during the two seasons could have affected the nutritive values.

The quality of proteins in a diet can be measured by its protein efficiency ratio. There was a general tendency for a low P.E. ratio to be associated with a high protein content (Table III). This slight trend is suggestive of the results obtained by Haydak (1953) with cockroaches. He found that the P.E. ratio decreased with increased dietary protein level and with increased age of the roaches.

Another evaluation of protein quality is given by the percentage of consumed protein retained in the tissues. The poorer materials (e.g., supplemented greasewood pollen) had higher nitrogen-retention values (Table IV) but lower P.E. ratios (Table III) than waterleaf and alfalfa pollen.

The amount of nitrogen contained in the adult bee is directly related to its weight. The percent nitrogen in the dry matter of the bee is inversely related to the weight of the bee. This could indicate that on the better diets (as shown by the size of the bee) there was more storage of non-nitrogenous materials. Since glycogen and fat can be derived from protein, it is possible that the larger bees showed lower nitrogen retention and higher P.E. ratios because some of the excess of amino acids was converted into glycogen or fat.

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# The Significance of Some Honeybee Dances

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## ABSTRACT

Solicitation to grooming by honeybees has been designated as a "grooming invitation dance", although previously described by Haydak as a "shaking dance" and by v. Frisch as a "Putztanz" (toilet or cleansing dance). The invitation consists of a rapid shaking of the body from side to side by a worker of hive age which then may be groomed by another of hive age, although some general groomers may continue to groom a series of workers (not field bees) without invitation. The latter indicates that this prominent activity has a definite niche in the economy of the hive, possibly the collection of a material used in brood rearing.

Description and conditions when found with evidence as to possible significance are given in support of the revised names of "spirit-tap", "pep-tap", or "D-VAV dance" (dorsal-ventral abdominal vibration), previously described by v. Frisch as "trembling bees" (Zitternde Bienen) and by Haydak as a "joy dance", a "good-time dance" or "dance of contentment". Tapping is performed by workers of field-duty age, occasionally at hive entrance, but more commonly on combs, at all hours of day and night, in flight and non-flight weather, in winter and summer, even in queenless colonies and to those at the point of starvation. Only instances of no tapping seem to occur when colonies have no needs or desires. During nectar- and pollen-gathering periods some gatherers repeatedly tap dance between field trips, sometimes interspersed with waggle-dances. Tapping was observed at an earliest age of 9 days and an oldest age of 151 days, the latter an over-wintering bee. In summer, many bees perform the dance during the last days of their life span. Normally, tapping is not done on the queen, but may be observed previous to but not immediately before the issuance of a swarm. Evidence indicates that D-VAV bees possibly are the control bees, having something to do with the "Spirit of the Hive".

The scope of this paper will include only the grooming invitation dance, with the responses to it, and the D-VAV dance ("spirit-tap" or "pep-tap"). The author (1953, 1955) has suggested these names as being more descriptive and definitive than names proposed by others. In the first instance, "shaking" (Haydak 1929, 1945) might be incorrectly applied to any of several other dances, while trembling (Frisch 1923) might be assigned to any shaking movement performed by bees.

## GROOMING INVITATION DANCE

By "grooming invitation dance" I refer to the rapid shifting of the worker's body, from side to side, apparently as a result of the alternate throwing of one of the second pair of legs upward beside the thorax and drawing it downward over the hairs in a combing-like operation. Thus an unstable side-rolling motion is given to the body, which may be misinterpreted as one of the forms of motion used to create cluster heat. The grooming invitation should not be confused with the "massage" type of dance described by Haydak (1945) which results in a treatment in which the responders use their antennae and front legs in a massaging manner on the body and legs of the affected bee.

In the case of the grooming invitation, the "barber" or "groomer" (Milum 1947) accepts the invitation, usually starting to work by climbing over the abdomen, pushing its mandibles and the head beneath the wings, usually with very little grooming until the constriction between the thorax and abdomen is reached, with a short interval of grooming in this region followed by a prolonged concentration on the hairs of the thorax behind the attachment of the wings. The actual work seems to consist of combing or sliding the hairs between the mandibles, but at times there appears to be an actual "nipping" or "clipping" action. At intervals, the "barber" backs up slightly and seems to be cleaning her mandibles with her front legs. I have noted a time interval of six

and one-quarter minutes for grooming of one bee, while a "general groomer", acting without invitation and upon a number of bees in succession, has been observed for a continuous period of 31 minutes. In another instance one groomer "barbered" 26 bees in 25 minutes. Even drones may be groomed if they happen to be in the brood nest area where grooming is usually performed.

The grooming invitation dance may be made as early as one day of age and accepted by bees as early as two days of age. It is an activity of bees of hive age. Grooming and grooming invitations may continue long after the cessation of brood rearing in the fall, but it should be remembered that fall reared bees are still physiologically "young". Field bees do not give the grooming invitation when their bodies are contaminated with pollen; their own cleansing activities after each flight are of such slow tempo that the groomers are not attracted. A young bee that happens to give its grooming invitation among a clustered group of old bees usually attracts no attention, yet we have observed instances of apparent resentment by resting field bees.

When the title of this paper was presented for this program, I had hopes of being able to give a proven analysis of the correct significance of the grooming invitation and its response, but up to now I can only suggest some possible explanations. Since grooming is chiefly performed on the thorax of young bees, with concentration on the heavily haired areas back of the wing bases, one might think that the groomers simply are removing the hairs because they are a flight hindrance? But the extended grooming by "general groomers" would seem to indicate that the hairs or some secreted substance is being collected for some useful purpose in maintaining the colony organization or the economy of the hive, possibly being used in the cell cappings of brood. This diligent action must have a definite and useful purpose, it can hardly be without value.

#### D-VAV DANCE

The second dance that I wish to consider is the D-VAV dance which may possibly be assigned the names of "spirit-tap" or "pep-tap" dances if our surmises eventually are proven to be true. By D-VAV, I mean a dorso-ventral abdominal vibration performed by a worker, usually by grasping with its front legs, the head, thorax or abdomen of another bee, although sometimes contacting only with the antennae, or without contact when the intended recipient moves out of reach. Occasionally an old bee that has been a tapper will perform a feeble D-VAV without any attempt at making contact. Hereafter, a unit of vibration, a single tapping, will be referred to as the sort of air-hammer movements in which the abdomen of the dancer is vibrated rapidly in a dorso-ventral direction 7 or 8 times in about eight-tenths of a second, then moving on to others, upon whom the vibrations are repeated at frequent as well as variable extended intervals. Occasionally under crowded conditions, the act may be repeated on the same bee. On the other hand, I once observed 25 consecutive rapidly repeated tapplings on a worker that was somewhat isolated from the cluster.

Tapping is exhibited on many occasions, at all hours of the day and night, at all seasons, with and without flight in progress, even in queenless colonies and those at the point of starvation, these latter instances indicating that they are not "joy", "good time", or "contentment dances". Furthermore, over a span of five years, there has been a period during the fall of each year when tapping could be found only infrequently, once for a period of two weeks when the observation hive had been fed heavily and was well supplied with honey. Brood rearing was practically over, there was no flight, there were no apparent needs or desires, there was no hurry and scurry, "not even a dancer was stirring". There was "contentment" but there was no dancing.

#### D-VAV AND WAGGLE DANCES COMBINED

Over a period of many years, I have on numerous occasions found a mixture or interspersing of D-VAV dances with waggle and with crescent dances by returning field bees, yet at times these may not be found. A few combinations by individual dancers follow: 314 D-VAV and 78 waggle-runs in 21 minutes (some not counted), 48 D-VAV and 33 waggle-runs in  $5\frac{1}{2}$  minutes, 42 D-VAV and 33 waggle-runs in  $2\frac{2}{5}$  minutes, and 111 D-VAV and 120 waggle-runs in  $11\frac{1}{2}$  minutes. In the latter instance, the two kinds of dances were nearly completely alternating, while in the first

case, the returning, loaded field bee started out with waggle runs only, then shifted to alternating dances, with no waggle runs after the first 100appings.

### D-VAV WITH RESPECT TO THE QUEEN

Ordinarily a roaming tapper will not enter the circle of royal attendants, but if it does it backs out quickly. On the other hand, in four different years I have observed tapping of the queen by numerous workers previous to the emergence of a swarm. In one instance, numerous workers repeatedly tapped the queen the second night before the swarm emergence, some on the next day, but none on the day of the swarm's emergence, which would seem to indicate that D-VAV had nothing to do with the actual emergence of the swarm. In another year, no tapping of the queen could be found, yet there was tapping of workers on the queen cells and on the cells themselves as well as two succeeding virgins that headed the second and third swarms. A third virgin was not tapped, apparently because brood had been removed, thus curtailing swarming, with this virgin heading the colony, after which observations during 72 days from July through December usually noted tapping by roamers but none on the queen. One of my students and I, each separately, have observed tapping of a queen after release from cage confinement. On one occasion a single tapping was observed on a laying worker, she being one of two in a small nucleus, each surrounded by a circle of royal attendants.

### AGE OF D-VAV BEES

Working with marked bees of known ages as well as by exchanging brood of different colored races, observations indicate that D-VAV is not a duty of young bees but one of bees of field age or at least old enough to perform such duties. However, tapping is not necessarily connected with field duties since, as previously indicated, it may be executed in the winter cluster, at night, and on cold, cloudy or rainy days when there is no flight. Some observations on age of tappers follow: of 20 tappers in 1948, none of the Italians were under 10 days of age and all Caucasians were over 15 days; a Carniolan tapped as early as 45 and as late as 52 days in July; in 1949 Italians tapped as early as 12 days and Caucasian as late as 45 days; an Italian tapped on 7 of the last 8 days of its apparent 39 day life, possibly earlier; in 1950, one Italian of a group tapped at 9 days and the last at 38 days of a total span of 42 days for the group; in 1951, 4 Caucasians tapped after 38 days, the last at the 44th of a 52-day life span. In 1952, some members of a group of marked bees tapped between the 14th and 39th days of a total span of 40 days. One Caucasian of a group wintered in an Italian colony tapped after an age of at least 151 days. Our previous suggestion that young bees might be induced to tap at an earlier age than 9 days as here noted has been confirmed and reported in personal correspondence by Mr. W. Wittekundt, a student at the Institute for Bee Culture in Bonn, Germany. This conforms to the observation of Wiltse (1882) who reported that young bees will start field duties as early as four days of age when older field bees are not available in a colony made up of recently emerged bees.

### WHAT IS D-VAV

While with many kinds of described dances, a proper interpretation is possible through observations of the responses of the other bees involved, in the case of bees upon whom D-VAV has been performed there is no immediate response to the dance, i.e., so far as we are able to note. Yet we cannot agree with one writer who has concluded that this movement means nothing in bee language. Its prevalence and absence under variable conditions indicates that it may have a definite niche in the organization of the colony. The observations here reported give some indication that D-VAV is really "spirit-tapping" or "pep-tapping", possibly by "control bees" of field-duty age. Although an exact message may not be conferred by the tapper, perhaps tapping serves as a general inspiration on all occasions, even to the queen, to continue or keep up the work of the colony. Its manifestations in times of activity, its absence in times of low colony activity or needs may indicate that herein lies "the spirit of the hive".

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# A Microinjection Technique for the Study of Bee Diseases

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## ABSTRACT<sup>1</sup>

*A critical method for the study of bee diseases utilizing a microinjector with a 30-gauge needle and an inoculating volume of 0.003 ml. is described. Honey bee larvae, pupae and adults can be injected by this method without mechanical damage. A minimum of working material and time is required and exact inoculating dosages of microorganisms or therapeutic drugs can be used.*

*The same equipment is also used for the detection of insecticides in honey bees. This is accomplished either by topical application or microinjection of exact amounts of extracted toxic material on or in test honey bees.*

<sup>1</sup> The complete text has been submitted to the *Journal of Economic Entomology*.



# The Use of Bacteriophages in the Analysis of the Foulbrood Diseases<sup>1</sup>

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## ABSTRACT

The laboratory diagnosis of American or European foulbrood disease is normally uncomplicated and straightforward. However, circumstances sometimes arise when it is desired to know more than just the species of bacteria involved, e.g., a given outbreak of disease may appear especially virulent, or resistant to treatment, or may appear to have been introduced from an outside source resulting from importation of bees or equipment. In such cases, one would like to be able to establish the identity of a particular strain of the bacteria associated with the unusual condition and base further studies on this identification. With this aim in mind, work was begun on the detection and isolation of specific bacteriophages from *Bacillus larvae*, cause of American foulbrood disease, and *Bacillus alvei*, commonly associated with European foulbrood disease.

The bacteriophages were isolated, and their specificities studied, by culture of bacilli from different sources in contact with each other. In addition, phage elaborated by some of the strains growing in single cultures in broth media were tested for activity on bacterial cells from other single cultures. Lytic activity using either procedure resulted in formation, in sensitive strains, of predominantly large plaques (2 - 3 mm) in the *B. larvae* system, and smaller (1 mm) plaques in the *B. alvei* system when plated on agar plates.

Strains of bacteria differing from each other with respect to bacteriophage production and sensitivity were demonstrated in both species. One strain of *B. larvae*, obtained from a colony from the State of Georgia, said to have a sulfathiazole resistant American foulbrood infection, yielded bacteriophage with activity for a large number of other strains of *B. larvae*. On the other hand, three strains obtained from Saskatchewan, Canada, produced no detectable phages.

## INTRODUCTION

Changes in apicultural practices in recent years have been reflected in changing needs in the diagnosis and control of the honeybee diseases. Shifting agricultural crop composition has dictated the movement of bees to and from various regions with the resultant movement to some degree of the associated honeybee diseases. Chemical control of some of these diseases has had its influence on diagnosis, as the problem of latent infection becomes more difficult to study, and the possibility of appearance of drug-resistant or otherwise altered microbial pathogens must be considered.

The search for bacteriophages for some of the honeybee pathogens reported here has been prompted in part by the considerations mentioned above. Bacteriophages, or bacteria-destroying viruses, have been found with activity for a great variety of bacterial species or subspecies. While the most tempting prospect in the study of these bacterial viruses has been their prophylactic use against bacterial diseases, their greatest value has actually been in the detection and identification of bacterial species, and — of importance here — the separation of species into sub-specific types or groups. This separation is made possible by the occurrence of a series of phages each with specific activity only for certain strains of a species. If one has a number of strains of phage with different specificities, a separation of the host bacterial species into phage types is possible. The utility of such a separation is in some bacterial species quite apparent, as factors such as pathogenicity, drug resistance, and source of the bacterial culture may be found associated in some way with the phage type of the strain under study (Blair 1956). Thus, the purpose of this research is to determine, in successive stages, the presence of bacteriophage for the species of honeybee pathogens or associated saprophytes, the separation of the species into types by bacteriophage typing, and the

<sup>1</sup>Paper No. 3674, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

relation, where possible of such phage types to characteristics of the diseases under study with respect to their virulence, drug response, and distribution. This report is concerned with the detection and lytic patterns of bacteriophages for *Bacillus larvae*, cause of American foulbrood disease (AFB) and for *Bacillus alvei*, an apparent saprophyte associated with European foulbrood disease (EFB).

## HISTORICAL

Morgenthaler (1949) quoted Baumgartner as stating that bacteriophages "were very important" in relation to *B. larvae*, but no further details were given concerning them. Smirnova (1954), in a report made available since the presentation of this paper at the Congress, stated that *B. larvae* phages of univalent and polyvalent activity could be obtained from larval residues infected with AFB, and that the polyvalent phages were useful for prophylactic as well as diagnostic value.

Krasikova (1956) reported the results of an extensive survey of plant nectars in the Soviet Union. She reported the presence of *B. alvei* phages active for many of her cultures in a large proportion of the nectars sampled. She ascribed the curative effect that a strong nectar flow may often have on EFB-infected colonies to the presence of these phages.

First details concerning the *B. larvae* phages studied at Minnesota appeared recently (Gochnauer, 1955) and this report extends in some further detail the work then reported.

## BACILLUS LARVAE PHAGES

### METHODS AND RESULTS

Detection of *B. larvae* phage at Minnesota resulted initially from the use of the cross-hatch agar plate test. Strain 11, received from Georgia, and stated to come from a sulfathiazole resistant infection, was streaked on a liver infusion nutrient agar plate across a streak from strain 12, received from Minnesota. No basic difference with respect to sulfathiazole resistance *in vitro* has been obtained for these two strains. However, upon incubation of the cross-hatched plate, plaques or well defined circular areas of lack of growth in the midst of growth appeared at the junction of the streaks. This was the first indication that these two strains differed in any substantial way, and suggested that one (lysogenic) strain was producing bacteriophage to which the other strain was sensitive.

To determine which strain produced the phage, and to characterize other strains by their reaction to the phage, a bacteria-free phage preparation was made up. A plaque from the cross-streak plate was removed aseptically and placed in a tube of liver infusion nutrient broth. Growth of the bacillus proceeded upon incubation of the tubes at 37°C and the phage presumably developed on the sensitive strain. At the end of the incubation period, when good bacterial growth was evident, the bacteria were removed by filtration of the broth through a Corning UF grade sintered glass filter. Aliquots of the filtrate were added separately to each of the two parent cultures, which were then plated individually on liver infusion nutrient agar plates.

At the same time, the filtrate prepared was tested for its activity for other *B. larvae* strains and a preliminary separation made (Gochnauer, 1955). The results are repeated here in Table I.

### PHAGE PRODUCTION BY *B. LARVAE*

Since the first results indicated that at least one strain of *B. larvae* produced detectable numbers of bacteriophage in a mixed culture, some strains were examined for their ability to produce phage in single culture. For this purpose, a number of strains were grown in brain heart liver infusion broth and the bacterial cells removed from a portion of the culture by centrifugation. This was done in 15 ml tubes in the Servall SS-1 centrifuge operating at top speed for 30 minutes. An aliquot (0.03 ml) of supernate was mixed with an aliquot (0.1 ml) of broth culture, allowed to adsorb for 30 minutes, and then mixed with 2 ml BLH agar in a sterile 16 × 150 mm culture tube. The whole was slanted, allowed to harden, and incubated for 3 days at 37°C. Each tube was examined for the presence of plaques, and some of the results are noted in Table II. There appear to be three types indicated by phage reactions of the cultures

TABLE I. Activity of Mixed Culture Filtrate  
for Individual *B. larvae* Strains.

Origin of scale sample	Plaque formation with phage
12. Minnesota	—
11. Georgia	+
1. Ohio	+
2. Pennsylvania	+
3. West Virginia	—
4. Wisconsin	—
5. Texas	—
6. Colorado	—
7. Iowa	—
8. Kentucky	—
9. Utah	—
10. California	—

tested. Strain 12 and C appear alike, and are related geographically to some degree. (Table IV). They are sensitive to phage from other cultures, but produce no phages with activity for any of the test bacterial cultures. Strains 47 and 54 appear alike both in activity of their filtrates and in sensitivity of their cells to filtrate. They are not geographically related as to source. Strain 11 is taken from the same Georgian source that was reported in Table I and is distinct from the others. Apparently the report of the sensitivity of strain 11 to bacteriophage was in error, and strain 12 was the sensitive culture.

TABLE II. Plaque-forming Activity of *B. larvae*  
Broth Culture Supernates on *B. larvae* Cultures.

Culture	Supernate from					
	11	12	C	47	54	11 × 12
11.	—	—	—	—	—	—
12.	+	—	—	+	+	+
C.	+	—	—	+	+	+
47.	+	—	—	—	—	+
54.	+	—	—	—	—	+

This is not to say that all tests of these filtrates give reactions as seemingly well defined as those in the table. For example, a spot plate test of these filtrates (for explanation see section on *B. alvei* phages) demonstrated the activity of supernate from strain 11 quite adequately. However, the activity of supernate 47 on cultures 12 and C, as shown in Table II, was not demonstrated by the spot plate method. The quantitative aspects of the method may be involved here, as plaque counts indicated a yield in the range of 100 plaque-forming particles per ml in some of the single, lysogenic cul-



tures of *B. larvae*. The spot plate test is limited in volume to about 0.01 ml per droplet applied, and may well have missed low levels of phage present.

BACILLUS ALVEI STUDIES

The demonstration of phage in *B. larvae* cultures led to attempts to demonstrate similar phenomena in *B. alvei*.

METHODS AND RESULTS

The cross-streak method for detection of bacteriophage in *B. larvae* was not applicable to *B. alvei* studies. The latter organism's motility on agar plates and characteristic film forming growth tends to obscure plaques formed in sensitive cells. Some plaques were observed by spotting the test cultures at some distance from each other on the plate so that growth at the border between the films spreading from each spot was thin. The procedure was not satisfactory, however, and was abandoned for the purposes of this report.

The method adopted consisted of the agar plate spot test, in which the test culture was inoculated in the surface layer of an agar plate as follows:

Two ml of a 24 hr culture mixed with 3 ml agar were poured over a plate with a 20 ml agar base layer (Case "C" medium was used). Seitz filtrates prepared from 24 hour broth cultures of the strains used were placed with the aid of a capillary pipette at discrete intervals across the surface of the hardened and dried plate. The plates were covered with Brewer absorbent metal petri dish tops and were held level until the spots had dried to prevent running. After 24 hours at 37C, the plates were examined for the presence of plaques at the places where the droplets were applied. Identification of the droplets was maintained by suitable marking on the bottom of the dish, and by a record kept of relative locations as well. The results appear in Table III, and represent the appearance of one or more plaques at the site of the applied droplet.

TABLE III. Plaque Formation by *B. alvei* Culture  
Filtrates on *B. alvei* Cultures.

Cultures	Filtrates from								
	C <sub>1</sub>	C <sub>2</sub>	C <sub>4</sub>	S <sub>1</sub>	S <sub>3</sub>	W <sub>2</sub>	W <sub>3</sub>	M <sub>1</sub>	RC
C <sub>1</sub>	—	—	—	—	—	—	—	—	—
C <sub>2</sub>	+	+	+	+	+	—	+	+	+
W <sub>1</sub>	—	—	—	—	+	—	—	—	—
S <sub>2</sub>	—	—	+	+	+	—	+	+	—
S <sub>4</sub>	+	+	+	+	+	+	+	+	+
M <sub>1</sub>	—	—	—	—	+	—	—	—	—

It is evident that strains C<sub>2</sub> and S<sub>4</sub> were highly sensitive to most of the filtrates tested, but the data are compromised by appearance of plaques by filtrate of C<sub>2</sub> on test culture C<sub>2</sub> and filtrate S<sub>4</sub> on culture S<sub>4</sub> (not shown). Spontaneous appearance of plaques without added filtrate in these two strains has occurred under conditions not yet defined. The sensitivity of these two strains would seem to have value in separating them from the others studied although the nature of the cell-virus relationship remains obscure. The action of filtrate prepared from red clover nectar (RC in Table III) on these two strains appears positive. Caution, however, needs to be exercised in interpreting this result to mean that the nectar itself harbors bacteriophage. Further work on this phase of the problem is needed.

On prolonged incubation, the plaques formed on Culture S<sub>4</sub> were filled with discrete, non-spreading colonies. Microscopic examination of smears from the colonies showed typical palisade arrangement of spindleshaped sporangia characteristic of *B. alvei*. Subculture of the colonies on agar slants resulted in formation of further discrete

TABLE IV. Source of Strains Studied.

<i>Bacillus larvae</i> strains		Obtained from:	Remarks:
1.	Ohio	A. S. Michael, USDA	
2.	Pennsylvania	"	
3.	West Virginia	"	
4.	Wisconsin	"	
5.	Texas	"	
6.	Colorado	"	
7.	Iowa	"	
8.	Kentucky	"	
9.	Utah	"	
10.	California	"	
11.	Georgia	H. Studier, Georgia	(Sulfa resistant?)
12.	Minnesota	R. Klein, Minnesota	
13.	Leipzig, East Germany	W. Fritzsche	
47.	Wanganui, New Zealand	"	
54.	Moscow, USSR	"	
C.	Caragana, Sask., Canada	S. E. Bland	
<i>Bacillus alvei</i> strains			
C <sub>1</sub>	Monte Vista, Colorado	J. O. Moffett	
C <sub>2</sub>	Durango, Colorado	"	
C <sub>4</sub>	Monte Vista, Colorado	"	(Streptomycin and Terramycin resistant?)
W <sub>1</sub> -W <sub>3</sub>	Greenhouse colony, Madison, Wisconsin	J. O. Moffett	
S <sub>1</sub>	Guernsey, Sask.	S. E. Bland	(Recent infection — 1955)
S <sub>2</sub>	Porcupine Plain, Sask.	"	(From one of first outbreaks in Sask.)
S <sub>3</sub>	Melfort, Sask.	"	
S <sub>4</sub>	Ridgedale, Sask.	"	
M <sub>1</sub>	Minnesota	Source not stated	

colonies, in contrast to the spreading, diffuse growth of normal *B. alvei* cultures. Apparently the cultures contained phage resistant variants characterized by a lack of motility on agar surfaces. Appearance of such phage resistant types in phage sensitive *B. larvae* cultures has not yet been observed.

GENERAL DISCUSSION

It seems plain that parasitism of bacterial cells by bacterial viruses or bacteriophage exists in *B. larvae* and *B. alvei* cultures, as in other bacterial species. The nature of this relationship is far from being defined quantitatively here. Such problems as the physical-chemical optima for adsorption of the virus upon the cell, the penetration and destruction of the cell and multiplication of the virus in the latter process are not defined at this point. Such definition is desirable from the viewpoint of a better understanding of host-virus relationships that exist as well as in the practical application of improving the sensitivity and reliability of the test reactions as we try to relate one culture to another.

As progress is made in separating strains of *B. larvae* and perchance *B. alvei* as well, progress will have to be made in describing the actual infections as they occur in the field. Little data is available concerning most of the infections from which these few samples were taken.

Krasikova's suggestion that *B. alvei* phage in plant nectars is responsible for the remission of EFB during the nectar flow requires first, that *B. alvei* be an important link in the pathogenesis of the disease, and second, that phage-resistant cells that may arise under the influence of exposure to nectar-born phage be non-pathogenic. However, if confirmation of her experimental results can be obtained, it would indicate the widespread nature of *B. alvei*, and perhaps aid in an understanding of *B. alvei*'s role as a secondary invader in the disease. Before a culture of *B. alvei* can be accepted as an indicator of the presence of bacteriophages in nectars, honey, and other materials, however, the stability of the culture with respect to lysis under the influence of added phage-free substances should be studied.

The isolation of a phage-resistant strain of *B. alvei* from the highly unstable cultures may give us a variant with interesting properties for further investigation of the nature of phage activity on *B. alvei*.

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# Comparative Susceptibility of Larvae of Different Stocks of Honey Bees to American Foulbrood When Reared by the Same Nurse Bees

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## ABSTRACT

A comparison between two different stocks of honey bee larvae was made by inoculating spores of *Bacillus* larvae into the food in 100 individual brood cells of each stock with a micrometer syringe at the same susceptible age, rearing the brood of both strains simultaneously in adjacent combs in the same healthy broodnest, then preventing removal of disease after the brood was sealed. In 43 such comparisons involving 13 stocks during 3 years, there was no consistent relationship between stocks and their susceptibility to American foulbrood. There were extreme variations in the percentages of diseased brood cells within individual stocks, and even in single colonies. The rate of larval development of two stocks reared simultaneously by the same nurse bees frequently was different, but the percentages of larvae sealed on the 8th day were not correlated with the percentages of diseased cells at pre-emergence. Larvae of 3 stocks were highly susceptible within 18 hours after hatching, but showed a very rapid decrease in susceptibility between the ages of 18 and 30 hours, and were immune beyond the age of about 42 hours. Diseased larvae may not die until after their cells are sealed. The exact age at which a larva ingests spores from its contaminated food probably affects its ability to resist infection, and may explain the wide variations in percentages of diseased cells reported. Stock resistance apparently is not due to larval resistance to American foulbrood, at least in the hybrid stocks studied.

Certain strains, or stocks,<sup>3</sup> of honey bees (*Apis mellifera* L.) are more resistant to American foulbrood than others, as observed by Lineburg (1925), Bixler (1926), and Richmond (1935). Park (1936) and Park et al. (1937, 1939) demonstrated that adult bees of resistant stocks are more efficient than those of susceptible stocks in cleaning out diseased brood. They may even tear down cell walls and rebuild the comb, thus disposing of infectious material. Tarr (1937) found that spores, but not vegetative cells, of *Bacillus* larvae produced infection when sprayed on brood combs. Tarr (1938) was unable to produce infection by inoculation of individual brood cells, most of which contained old larvae, and suggested that adult bees play an important role in the disease. Woodrow (1941a, 1942) found that larvae of resistant and susceptible stocks appeared equally susceptible to American foulbrood. Both became infected only during their early life, within 2 days and 5 hours after hatching. Many of them did not die until after their cells were sealed at the age of 5 to 6 days. This relationship of age to susceptibility was confirmed by Katznelson and Jamieson (1950), who showed that it also holds true for queen larvae. Woodrow and Holst (1942) presented evidence that the resistance of certain stocks is due primarily to the adult bees detecting the disease in its early stages and cleaning out the diseased larvae before the bacteria attain the infectious spore stage, that is, before the decaying larvae become "ropy". Sturtevant and Revell (1953) demonstrated that adult bees of resistant stocks remove a higher percentage of spores from liquid food that they ingest, regurgitate, and store than do bees of susceptible stocks.

Preliminary comparisons by the author at Laramie, Wyoming, in which larvae of similar ages from different stocks of bees were reared simultaneously in the same heavily diseased colony, sometimes showed marked differences in the percentages of larvae that developed American foulbrood. These differences were especially noticeable when the brood combs were taken away from the colony shortly after sealing and reared in an incubator to prevent adult bees from removing diseased larvae from sealed

<sup>1</sup>A. P. Sturtevant and I. L. Revell assisted in these experiments.

<sup>2</sup>In cooperation with the University of Wyoming (Wyoming Agricultural Experiment Station, Journal Paper No. 82).

<sup>3</sup>In this paper the term "stocks" is used to include hybrids, because the term "strain" has a genetic connotation of pure breeding which may or may not have been the case for various strains cited in the literature.

cells. For example, only 30 percent of the sealed larvae of a stock having a history of resistance but 87 percent of those of a second stock having a history of susceptibility became diseased when exposed to a naturally infected comb in which 98 percent of the sealed larvae were diseased. Since nurse bees of the same susceptible stock cared for larvae of both stocks, it appeared possible that there might be differences in the physiological resistance of the larvae themselves, as well as in the house-cleaning activity of the adult bees.

## METHODS

In order to compare the resistance of larvae of different stocks of bees to American foulbrood, rather than entire colonies whose resistance might depend on adult behavior, individual cell inoculations similar to those made by Woodrow (1942) were used, and in each comparison larvae of two stocks were reared simultaneously by the same nurse bees.

Queens of two stocks were each confined to single empty brood combs by a queen-excluder cage, or to a small area of a comb by a wire-cloth push-in cage, during the same period of time, and then were prevented from laying any more eggs in those combs. The two brood combs containing eggs from different stocks were then placed in adjacent positions in the same healthy colony, where they were left until shortly after the brood was sealed. However, in the first four comparisons in 1953 the eggs and larvae were reared by nurse bees of their own stock before inoculation. One hundred larvae of each stock were inoculated individually with an aqueous suspension of spores of *Bacillus larvae* by touching a droplet of the inoculum to the food in the base of each brood cell when the larvae were of known susceptible age. The exact position of each inoculated cell was recorded by means of Woodrow's (1941b) cell-locating frame, so that it could be identified and re-examined at any future date. Uninoculated larvae in alternate rows of cells were also recorded and examined. Soon after all the larvae were sealed, usually on the 9th day after egg laying, the combs were taken from the rearing colony and kept inside wire-screen cages in an incubator at 34°C. (93°F.) to prevent adult bees from removing diseased larvae after they had attained the sealed stage. Shortly before emergence, usually on the 18th day after egg laying, the cappings were opened with a needlelike tool to determine whether the cells contained healthy or diseased brood.

In 1953 and 1954 queens were confined for 24 hours and larvae were inoculated at the theoretical ages of 6 to 30 hours. The minimum and maximum ages of the larvae in each comb were computed on the assumption that all eggs hatched 72 hours after laying, although it is known that slight variations occur. In 1955 queens usually were confined for 6 hours only, and the larvae were inoculated at the theoretical ages of 18 to 24 hours, to reduce the age differences between the youngest and oldest.

The micrometer syringe used in the first 2 years had a thumbscrew device to operate the plunger (Woodrow 1942); so the size of droplet was controlled by hand. It was calibrated to deliver about 100 spores per droplet. In 1955 a new micrometer syringe was used, designed after that described by Woodrow (1949), in which the droplet size was more uniform because the movement of the plunger was controlled by a geared thumb-screw passing over a ball bearing supported over a spring. This instrument was calibrated to deliver about 350 spores per droplet. The spore suspensions were prepared from a known weight of dried and powdered American foulbrood scales containing approximately known numbers of spores, serially diluted in known volumes of distilled water.

Over the 3-year period 43 comparisons involving 13 stocks of bees were made. Some of the stocks had known histories of resistance or susceptibility to American foulbrood, based on inoculations of entire colonies by feeding them 500,000,000 spores of *Bacillus larvae* in 1 liter of sugar syrup, as described by Sturtevant (1949). The stocks tested and the year their queens were reared, were as follows: A'50, B'51 and D'51 were four-way hybrids reared by the Ohio Breeding Project on Kelley Island; C'53 and H'54 were commercial four-way hybrids from Kelley Island stock; G'52 and I'52 were four-way hybrids reared by the Ontario Breeding Project on Pelee Island; J'54, K'54, and L'55 were commercial hybrids originating from Iowa's Dadant "Starline" stock and advertised as resistant to American foulbrood; and E'53, M'55,



and N'55 were ordinary commercial Italians. All queens were naturally mated, those on the islands to drones selected by extreme isolation.

In ten of the 1955 comparisons, observations were also made on the percentages of larvae sealed at a given time, to compare their rates of development and their susceptibility to American foulbrood. Larvae of three stocks were tested for their susceptibility to American foulbrood at successive 6- or 12-hour age intervals when reared by nurse bees of their own strain.

RESULTS

Table I shows the percentages of diseased cells in the sealed brood of supposedly resistant or susceptible stocks after individual larva inoculations at the same age and

TABLE I — Comparative Susceptibility of Larvae of Supposedly Resistant and Susceptible Stocks of Honey Bees to American Foulbrood when Reared by the Same Nurse Bees.

Stocks whose larvae were compared		Stock of nurse bees that reared larvae of both stocks to sealing	Inoculation date	Percent of inoculated larvae removed before sealing		Percent of sealed cells found infected at pre-emergence	
Resistant	Susceptible			Resistant	Susceptible	Resistant	Susceptible
1953 (100 spores per larva, larvae 6-30 hours old at inoculation)							
A	B	A	Aug. 3	38	53	63	89
		B	Aug. 7	11	7	42	62
C	B	C	Aug. 24	12	40	18	67
		B	Aug. 28	3	48	19	85
		C	Sept. 14	31	50	36	80
C	D	C	Aug. 24	26	68	24	81 <sup>a</sup>
C	E	C	Aug. 28	39	21	75	38 <sup>a</sup>
1954 (100 spores per larva, larvae 6-30 hours old at inoculation)							
C	G	C	June 21	36	31	47	29
		G	June 25	41	43	27	28
C	H	H	July 2	8	4	15	2
		C	July 12	78	14	59	12
I	H	H	July 2	19	0	30	7
		I	July 12	11	5	18	9
		H	July 30	59	27	74	32
		I	Aug. 2	9	8	13	47
		H	July 30	31	29	34	26
		I	Aug. 2	5	2	11	17
1955 (350 spores per larva, larvae 18-24 hours old unless otherwise indicated)							
C	H	C	June 27 (0-24)	88	77	18	13
		H	July 1 <sup>b</sup>	61	12	26	5
		H	Aug. 15	11	11	70	27
		C	Aug. 26	16	22	76	60
J	H	H	Aug. 5	6	1	55	42
		J	Aug. 22 (0-18)	20	16	85	85

a A few cells of disease were observed in natural brood combs of colonies supplying eggs of susceptible stocks.  
b Larvae of stock C were 0-18 and of stock H 18-24 hours old when inoculated.

after rearing to the sealed stage by the same nurse bees. In 1953 brood of stocks with a known history of colony resistance to American foulbrood, with one exception, showed considerably lower percentages of infected cells than brood of susceptible stocks. The most striking difference was between resistant stock C, which had only 18 to 36 percent of diseased cells, and susceptible stock B, which had 67 to 85 percent, in three comparisons. However, in 1954 and 1955 supposedly resistant stocks sometimes developed higher percentages of diseased cells than supposedly susceptible stocks.

For example, resistant stock I had 74 percent of diseased cells when susceptible stock H had only 32 percent, and similarly resistant stock C had 70 percent of diseased cells when susceptible stock H had only 27 percent, in two of the comparisons when nurse bees of the susceptible stock reared the larvae of both stocks to sealing. Stock I showed a higher percentage of diseased cells than stock H in four comparisons, but a lower percentage in two other comparisons.

Variations in the percentages of diseased cells in different tests of the same stock, or even of the same colony, were extremely great, irrespective of their history. For example, resistant stock C had as low as 15 percent and as high as 76 percent, while susceptible stock H ranged from 2 to 60 percent of diseased cells. Moreover, there was no consistent relationship between the stocks and the percentage of larvae removed by the nurse bees before the brood was sealed. For example, from 12 to 88 percent of the inoculated larvae of stock C were removed before sealing when reared by nurse bees of resistant stocks, and from 3 to 61 percent were removed when reared by susceptible stocks.

Table II shows the percentages of diseased cells in the sealed brood when two resistant stocks, two susceptible stocks, or stocks of unknown history were compared.

TABLE II — Variations in Susceptibility of Larvae of Various Stocks of Honey Bees to American Foulbrood.

Stocks whose larvae were compared		Stock of nurse bees that reared larvae of both stocks	Inoculation date	Percent of inoculated larvae removed before sealing		Percent of sealed cells found infected at pre-emergence	
First stock	Second stock			First stock	Second stock	First stock	Second stock
1954 (100 spores per larva, larvae 6-30 hours old at inoculation)							
Both stocks resistant							
C	I	C	June 21	29	13	72 <sup>a</sup>	30
		I	June 25	7	20	26	25
J	I	J	July 19	5	15	22	42
		I	July 23	3	13	34	34
		J	Aug. 9	11	39	25	57
		I	Aug. 13	10	17	18	28
J	C	J	July 19	4	3	26	4
		C	July 23	9	8	23	29
		J	Aug. 9	15	20	28	69
		C	Aug. 13	11	14	25	34
1955 (350 spores per larva, larvae 18-24 hours old unless otherwise indicated)							
J	C	C	June 27 (0-24)	81	75	16	8
		J	Aug. 22	8	8	57	47
Both stocks susceptible							
H	K	H	July 29	10	8	22	10
		K	Aug. 8	3	6	28	54
		H	Aug. 8	5	16	26	74 <sup>b</sup>
Unknown stocks							
L	H <sup>c</sup>	H	July 11	1	4	15	18
		L	July 18 (0-18)	4	59	8	85
M	N	M	Sept. 2	32	4	62	44
		N	Sept. 12	57	34	78	41
		N	Sept. 2	9	5	55	53

a Colony of stock C supplying eggs and rearing brood had a few cells of disease in its natural brood combs.  
b Colony of stock K supplying eggs had a few cells of disease in its natural brood combs.  
c Susceptible.

Again great variations within stocks occurred. For example, stock C varied from 4 to 72 percent of diseased cells, and stock J from 18 to 57 percent. Moreover, stocks C and J had 4 and 26 percent of diseased cells in one comparison, but 69 and 28 percent

in another, apparently reversing their comparative susceptibility, even though nurse bees of stock J reared the larvae of both stocks in both comparisons.

Less than 0.1 percent of uninoculated larvae in alternate rows of cells became diseased, in spite of their proximity to the inoculated larvae. The data of tables I and II appear to indicate that colony resistance to American foulbrood is not associated with physiological resistance of the larvae<sup>4</sup>.

Preliminary observations in 1954 indicated that, when two queens of different stocks were confined for the same 24-hour egg-laying period, there sometimes were great differences in the rate of development of their larvae, even when reared simultaneously in adjacent combs in the same colony. In eight such comparisons larvae of one stock, which were obviously smaller at the time of inoculation than those of the other stock, invariably showed higher percentages of diseased cells than the larger larvae of presumably identical age. In one outstanding case about one-third of the brood of stock C was already sealed on the 8th day after egg laying, and two adult bees emerged before the oldest brood was 19 days 4 $\frac{1}{4}$  hours old. This is considerably less than the 20 $\frac{1}{2}$  days found to be the average time required for the development of worker bees (Milum 1930). Stock J, reared simultaneously in an adjacent comb in the same brood nest, had none of its larvae sealed by the 8th day, and none of its brood had emerged when examined  $\frac{1}{2}$  hour later than stock C. Stock C had 4 percent and stock J had 26 percent of its cells diseased. The apparent differences in rate of development might have been due to the two queens starting to lay at different times within the same 24-hour period.

In 1955 more exact data on the time of sealing were obtained in ten comparisons after the queens had laid eggs during only a 6-hour period. These data are summarized in Table III. Again there were differences in the rate of development between stocks reared simultaneously by the same nurse bees. However, there was no consistent relationship between time of sealing and percentage of diseased cells. In the first comparison of stocks H and K, brood of stock H developed faster, yet had more diseased cells, than brood of stock K; in the second comparison H developed faster and had less disease than K; while in the third comparison H developed more slowly and had more disease than K. Moreover, two stocks might show similar rates of development and yet have large differences in the percentages of diseased cells, as in the first comparison of stocks H and C. Conversely, the rates of development might be quite different and yet the infections could be identical, as in the comparison of stocks J and H. Incidentally, the inoculated cells usually were sealed a little more slowly than uninoculated cells in alternate rows of the same brood comb.

Data regarding the susceptibility of larvae at different ages are presented in Fig. 1. This graph shows a high susceptibility, averaging about 85 percent, among larvae less than 18 hours old, a very rapid decrease in susceptibility from 18 to 30 hours, a further gradual decrease from 30 to 42 hours, and no infection among larvae more than 42 hours old. These data confirm those of Woodrow (1942).

Although there appeared to be differences in susceptibility between these three stocks, extreme variations occurred within each stock. For example, in eight inoculations at the age of 18 to 24 hours, stock H showed from 5 to 60 percent of its cells diseased (see Tables I and II). The very rapid decrease in susceptibility between 18 and 30 hours may explain the wide variations obtained in the percentages of diseased cells among individually inoculated larvae, both within and between stocks. The exact age at which a larva ingests the spores from its contaminated food may affect its ability to resist infection.

### SUMMARY

In an attempt to determine if different stocks of honey bees (*Apis mellifera* L.) are more resistant to American foulbrood than other stocks because of differences not

<sup>4</sup> While this manuscript was being prepared, an important paper appeared on a similar study by W. C. Rothenbuhler and V. C. Thompson. 1956. Resistance to American foulbrood in honey bees. I. Differential survival of larvae of different genetic lines. *Jour. Econ. Ent.* 49(4): 470-475. They obtained evidence of differences between strains due to different levels of innate resistance of the larvae. They observed survival rather than disease. They did not prevent removal of disease by adult bees after the brood was sealed. They compared artificially inseminated queens of highly inbred lines rather than naturally mated queens of hybrid stocks. These differences may explain why their result differs from that presented here.

TABLE III — Comparison of Stocks as to Time of Sealing and American Foulbrood Infection when Reared by the same Nurse Bees.

Stock of nurse bees that reared larvae of both stocks	Stocks whose larvae were compared	Sealing of brood cells			American foulbrood Percent of sealed cells in inoculated rows infected at pre-emergence <sup>a</sup>
		No. days after egg-laying when examined	Percent of larvae sealed		
			Uninoculated rows	Inoculated rows	
H	H	8	44	25	22
	K	8	13	6	10
K	H	8	89	80	28
	K	8	39	34	54
H	H	8	?	0	74
	K	8	83	64	26
H	H	8	10	8	27
	C	8	10	4	70
C	H	8	51	43	60
	C	8	?	22	76
J	J	8 <sup>3</sup> / <sub>4</sub>	98	98	47
	C	8 <sup>3</sup> / <sub>4</sub>	100	100	57
J	J	8	76	69	85 <sup>b</sup>
	H	8	97	91	85 <sup>b</sup>
L	J	7 <sup>1</sup> / <sub>4</sub>	3	0	71 <sup>b</sup>
	L	7 <sup>1</sup> / <sub>4</sub>	8	3	80 <sup>b</sup>
M	M	8	63	62	62
	N	8	16	10	44
N	M	8	?	11	55
	N	8	?	77	53

a Larvae inoculated at age of 18-24 hours, unless otherwise indicated.  
b Larvae inoculated at age of 0-18 hours.

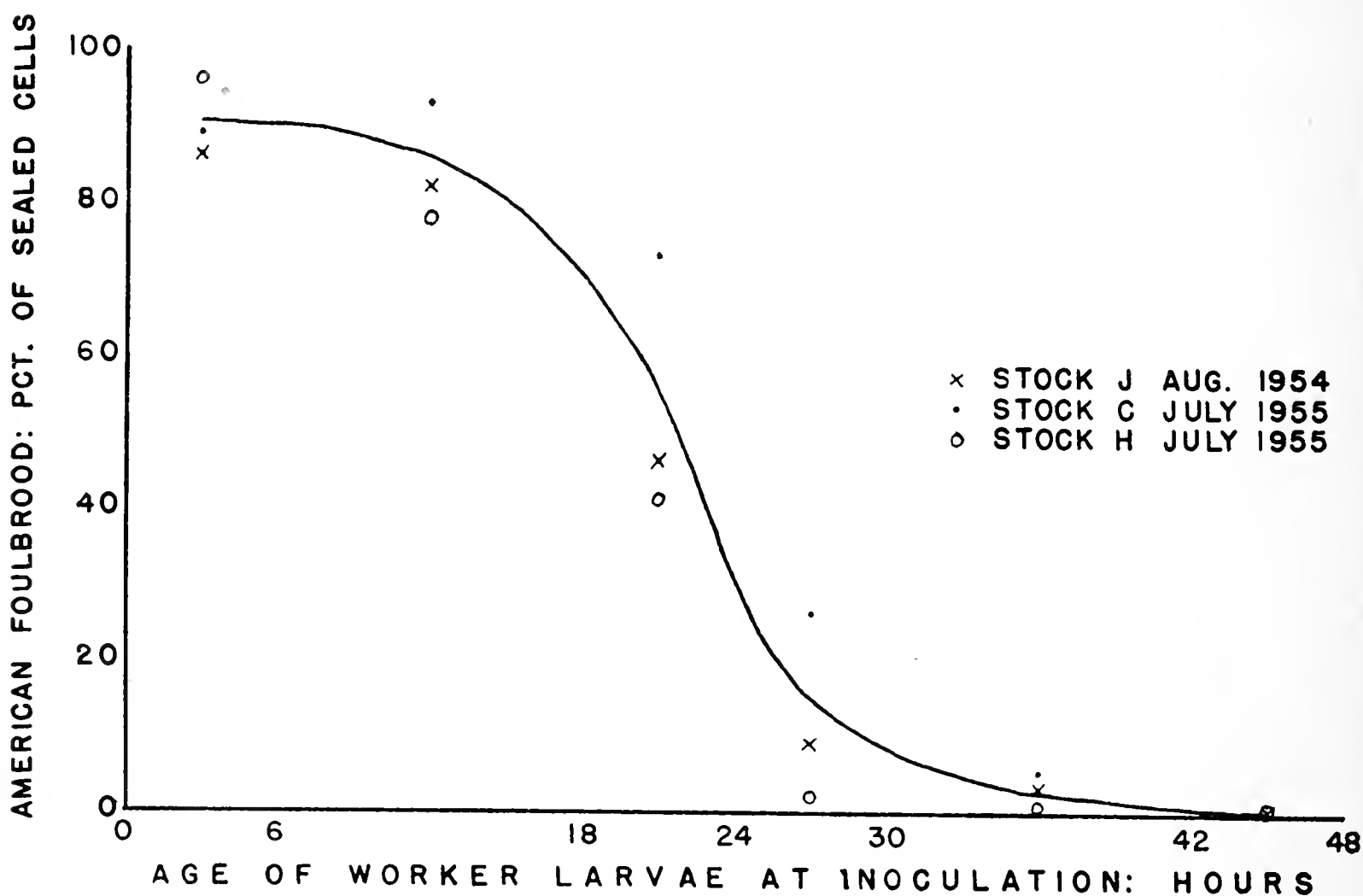


Fig. 1. Relation between age of honey bee larvae and their susceptibility to American foulbrood

only in the behavior of adult bees but possibly also in the physiological resistance of the larvae themselves, larvae of different stocks were reared in adjacent combs simultaneously by the same nurse bees. Larvae were individually inoculated at the same susceptible age. Removal of disease by adult bees after sealing was prevented by rearing the sealed brood in an incubator.

No consistent relationships were observed between larvae of different hybrid stocks and their susceptibility to American foulbrood. The percentages of diseased brood cells within the same stock, or even the same colony, were extremely variable. Larvae of different stocks frequently showed great differences in their rate of development, but the time of sealing was not a reliable index of their comparative susceptibility to American foulbrood. A very rapid decrease in susceptibility occurred between the larval ages of 18 and 30 hours. This probably explains the wide variations in the percentages of diseased cells reported. These experiments appear to substantiate previous literature which indicates that colony resistance to American foulbrood is associated with adult behavior in removing disease, rather than with physiological resistance of the larvae.

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# Observations on the Causal Agents of American and European Foulbrood and their Control with Antibiotics<sup>1</sup>

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## ABSTRACT

During the past few years emphasis in our laboratories has been placed on the metabolism of *Bacillus larvae*, cause of American foulbrood (AFB), on organisms associated with European foulbrood (EFB) and on the use and stability of antibiotics for the control of these diseases. A medium has been developed in which *B. larvae* grows well and produces abundant cells for metabolic work. This organism metabolizes glucose via the glycolytic route but also possesses enzymes of the hexosemonophosphate oxidative pathway. Acetic acid is an important breakdown product of glucose; pyruvic and lactic acids are also formed.

Repeated efforts were made to isolate the causal organism of European foulbrood from infected bomb. Young healthy larvae, and discoloured dying or dead forms were used for isolation on a wide variety of media. The most frequently encountered organism was *Bacillus alvei*. Very few healthy larvae yielded this bacterium whereas 75 per cent of those suspected of being infected with EFB contained this organism; many of these dead larvae showed no evidence of *Streptococcus pluton*, yet had the appearance and odour associated with EFB.

Apiary tests with various antibiotics showed that terramycin was effective against both AFB and EFB, whereas streptomycin was effective only against the latter. Achromycin also controlled AFB. Extensive tests on the stability of these and other antibiotics in honey and sugar syrup at 4° and 34°C. have been completed and indicate that streptomycin was the most stable, with achromycin next. Terramycin and penicillin were quite unstable especially at the higher temperature. The significance of these findings is discussed.

Studies on and controversies over the use of sulpha drugs and antibiotics for the control of various diseases of the honeybee, such as American and European foulbroods, and Nosema disease, have tended to draw attention away from the causal agents themselves. Yet comparatively little is known about them, and those causing European foulbrood and Nosema disease have not even been successfully cultured in the laboratory. Investigations at the Bacteriology Division in Ottawa have been concerned with both practical and fundamental aspects of the honeybee disease problem. Studies have been carried out on the control of these diseases with sulpha drugs and antibiotics and on the nutrition and metabolism of the organisms causing, or associated with the foulbroods such as *Bacillus larvae*, cause of American foulbrood (AFB) and *B. alvei* and *Streptococcus apis*, forms associated with European foulbrood (EFB). Various phases of these investigations have already been published and will be dealt with briefly, other aspects will be considered in somewhat greater detail in this paper.

## GROWTH AND METABOLISM OF BACILLUS LARVAE

*B. larvae* requires intact vitamin B<sub>1</sub>, purine bases such as xanthine, guanine or adenine and certain amino acids for growth (Lochhead, 1942; Katznelson and Lochhead, 1948). Additional factors are required for good growth in artificial media but these have not been identified as yet. The organism grows quite well in a yeast extract, tryptone salts glucose medium but without sporulating readily. Excellent and rapid growth has been obtained on Difco's brain liver heart medium with 1.5% agar; this medium favours germination of spores derived from AFB scale, particularly if its reaction is adjusted to pH 6.5 to 6.7. However, sporulation in this medium has not been as abundant or as consistent as desired; it was improved somewhat by the addition of skim milk but not of starch or charcoal, contrary to the observations of Foster and collaborators (Foster *et al.*, 1950).

<sup>1</sup>Contribution No. 425.

Growth of this organism in liquid media was, on the whole, poor but a medium consisting of yeast extract, peptone, inorganic salts and glucose supported excellent growth if the flasks were shaken continuously. Cells obtained from these shake cultures were used for metabolic experiments.

According to earlier work (Lochhead, 1928) *B. larvae* is a facultative organism, reducing nitrates and growing better, on the whole, under the somewhat anaerobic conditions obtaining in semi-solid agar. Yet its excellent growth on a shaker, without nitrate reduction, as compared with its poor growth in stationary flasks, accompanied by nitrate reduction, appeared to contradict the above conclusion. It remained therefore for metabolic studies to clarify this problem.

Metabolic experiments were carried out with intact cells and with cell-free extracts prepared by sonic vibration.<sup>2</sup> In brief, it was found that *B. larvae* metabolized glucose primarily via the glycolytic or fermentative route, with pyruvic and acetic acids as important products; lactic acid was also formed. The key enzymes involved in this pathway of glucose breakdown were also demonstrated by standard biochemical methods. These results support the original observations that this organism is indeed more a facultative than an aerobic form.

In addition to the enzymes of the glycolytic route, however, this organism possesses enzymes of the hexosemonophosphate oxidative pathway. That is, it is capable of oxidizing glucose-6-phosphate and 6-phosphogluconate in the presence of Coenzyme II or triphosphopyridine nucleotide, suggesting the presence of glucose-6-phosphate and 6-phosphogluconate dehydrogenases. The organism also contains enzymes which are capable of oxidizing rapidly ribose-5-phosphate, but to date it has not been possible to link this oxidation to the sedoheptulose-phosphate pathway. Further work is obviously required to clarify this problem but it is conceivable that the ability of *B. larvae* to grow rapidly on a shaker is related to its possession of this oxidative system.

### STUDIES ON EUROPEAN FOULBROOD

Repeated efforts have been made to culture the causal agent of EFB. Simple and complex media have been employed under aerobic and anaerobic conditions, at different temperatures and so on, without success. Our experience therefore is in line with that of most other investigators of this disease. As is well known, however, a number of the organisms found in association with this disease have been isolated and found to grow well on artificial media. These include *B. alvei*, *B. sphaericus*, *B. laterosporus*, and *Streptococcus apis*. Nutritional studies on *B. alvei* and *S. apis* (Katznelson and Lochhead, 1947; Katznelson, 1947) have shown that the former required vitamin B<sub>1</sub> as the only growth factor as well as a number of amino acids such as glycine, leucine and cystine. The latter had considerably more complex requirements for good growth in a synthetic medium. Pantothenic acid, nicotinic acid, pyridoxine and biotin were essential; folic acid was required by one strain which was also stimulated by vitamin B<sub>1</sub>. Various amino acids, such as valine, leucine and glutamic acid were essential and others stimulatory.

In the course of these studies large numbers of young, apparently healthy larvae from EFB comb, as well as discoloured, twisted, dying or dead forms were examined prior to the cultural tests. Most of these and all of the healthy larvae showed no evidence of *Streptococcus pluton*, yet had the appearance and odour associated with EFB. As usual the organism isolated most frequently was *B. alvei*. Very few "healthy" larvae yielded this organism whereas over 75 per cent of those suspected of being infected with EFB yielded it. In the light of such results the question again arises as to the possible involvement of this organism in this disease, and not necessarily as a secondary invader.

Several unusual bacteria were isolated in the attempts to culture *S. pluton*. These were quite fastidious organisms and were maintained with difficulty over a period of time. The predominant form morphologically resembled *Corynebacterium* or *Arthrobacter* types, and, in older cultures appeared to break up into units which resembled *S. pluton*. The second organism was also a short Gram positive, non-spore forming rod and had a decided tendency to remain attached after several divisions to form an

<sup>2</sup>See Mylroie and Katznelson.

irregular circle. These forms have not been identified as to species; however, it is interesting to speculate whether these types are frequently associated with EFB and whether the fragmentation of the former to produce "pluton"-like elements may not be confused with EFB itself.

CONTROL OF AFB AND EFB WITH ANTIBIOTICS

The problems underlying the use of antibiotics to control AFB and EFB are familiar to all those who have used these chemotherapeutic agents. Most of the work in this field, as carried out in Ottawa, has already been published and will only be summarized briefly. Of a large number of antibiotics tested in feeding experiments against AFB, (Katznelson, 1950; Katznelson and Jamieson, 1952), only terramycin and achromycin were shown to be effective in controlling this disease for an entire season (May to September. Katznelson *et al.*, 1955). The minimum amount of terramycin required in this connection was 250 mg. per gallon per colony. However, terramycin-treated colonies showed a recurrence of AFB the following season in contrast to sulpha-fed colonies which did not. Stability of the drugs in honey was considered as a possible clue to this phenomenon and will be considered shortly.

In experiments on the control of EFB (Katznelson *et al.*, 1952) streptomycin, chloromycetin, aureomycin and terramycin were tested. Streptomycin and terramycin were found to be effective in a variety of well-replicated tests. However, reports of recurrences after terramycin treatment again suggested the need for stability trials.

STABILITY OF ANTIBIOTICS IN HONEY<sup>3</sup>

It is obvious that the stability of compounds found to be effective against AFB and EFB is a very important consideration. It is possibly owing to their instability under the conditions prevailing in a hive that substances such as penicillin, though very

TABLE I — Stability of Antibiotics in Honey and Sugar Syrup (expressed as per cent of original at 0 time).

Antibiotic	Medium	(°C.) Temp.	Months			
			1	2	4	9
Erythromycin	Honey	4	91	83	64	54
		34	39	0	0	0
	Sugar	4	95	77	68	51
		34	37	0	0	0
Achromycin	Honey	4	45	36	32	22
		34	39	30	15	2
	Sugar	4	49	40	35	27
		34	39	30	10	2
Streptomycin	Honey	4	81	71	46	44
		34	75	67	25	13
	Sugar	4	70	69	36	40
		34	68	31	—	11
Aureomycin	Honey	4	95	32	45	43
		34	80	26	16	2
	Sugar	4	91	30	13	2
		34	—	0	0	0
Terramycin	Honey	4	69	30	22	14
		34	22	0	0	0
	Sugar	4	60	40	40	26
		34	22	0	0	0
Penicillin	Honey	4	17	8	0	0
		34	0	0	0	0
	Sugar	4	19	1	0	0
		34	0	0	0	0

<sup>3</sup>See Landerkin and Katznelson.

potent *in vitro*, are not particularly effective in the apiary. Experiments carried out with three sulpha drugs (Katznelson and Jamieson, 1954) showed that they were effective against AFB even after three years' storage in honey. Similar tests with terramycin (Katznelson *et al.*, 1955) indicated complete loss of activity when stored in honey for 6 months.

A more comprehensive experiment was then initiated in which a number of antibiotics were added to honey and to 50 per cent sugar syrup maintained at 4° and 34°C. and tests made at monthly intervals for potency by standard disc assay procedures. The results obtained are summarized in Table I. In every instance stability was greater at the lower temperature. Penicillin was the least stable compound under all conditions whereas streptomycin was the most stable. Achromycin and aureomycin showed some activity at the end of nine months whereas terramycin and erythromycin were no longer detectable after two months at 34°C.

### CONCLUSION

It is clear that much remains to be learned about the foulbroods and their control. However, our knowledge is increasing steadily and as the techniques of biochemistry, physiology and nutrition are applied to these problems they will undoubtedly be resolved.

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# Studies on the Manifestation, Control and Prevention of European Foulbrood Disease in Package Bee Colonies

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## ABSTRACT

*Examination of 1300 package bee colonies installed at different dates in 1954 and 1955 at Beaverlodge, Alberta, indicated that European foulbrood did not appear until approximately 5 weeks later. Of six antibiotics tested, oxytetracycline, streptomycin and erythromycin were effective in controlling European foulbrood, while chlortetracycline, cycloserine and puromycin were not. Preventive treatment of non-diseased colonies with 250 mg. of oxytetracycline or streptomycin gave complete protection against European foulbrood for a four-week period.*

European foulbrood (E.F.B.), a bacterial disease of honeybee larvae, has become a problem in the beekeeping industry in western Canada. Serious outbreaks of the disease have occurred in different sections since 1950. As E.F.B. spreads very rapidly, affecting colony build-up and honey production, prevention of the disease would be more practical than control, especially in commercial apiaries where examinations are sometimes infrequent. E.F.B. often becomes rampant before the beekeeper is aware of its presence. An economic and effective method of prevention or control of this disease is highly desirable.

Previous workers (Katznelson *et al.*, 1952; Moffett, 1953) found that the antibiotics oxytetracycline and streptomycin would control E.F.B. However, since the degradation of these and other antibiotics in honey or sugar-syrup varies (Katznelson *et al.*, 1955; Katznelson, 1956) it is important to time the treatments for most efficient use.

The prime objectives of these studies were (a) to determine the interval between the installation of the package bees and the manifestation of the disease, (b) to test other antibiotics in addition to streptomycin and oxytetracycline for effectiveness in control of E.F.B., and (c) to determine the period of time a preventive treatment of an effective antibiotic would give complete protection against E.F.B.

## PROCEDURE AND RESULTS

### MANIFESTATION OF E.F.B. IN PACKAGE BEE COLONIES

The experiments were conducted at Beaverlodge, Alberta, in 1954 and 1955. Most of the colonies used in these tests were supplied by the Smith Apiaries which had shown severe E.F.B. infection in 1953 so it was expected that the disease might be present the following year. Accordingly, 930 two-pound packages, imported from California, were installed in 1954 at five dates ranging from April 13 to May 7. In addition, 100 two-pound packages were installed April 23 and May 5 at the Experimental Farm in hive bodies which were apparently free from the organism(s) causing E.F.B. These colonies were examined at weekly intervals and the date recorded when symptoms of the disease appeared.

In 1955, similar observations were made on 170 colonies which had been hived on April 13 and May 13 in equipment that was contaminated with this brood disease in 1954. The results obtained in 1954 and 1955 are given in Table I.

Data in Table I indicate that a period of approximately five weeks (35-38 days) elapsed after hiving before E.F.B. symptoms were noted in the colonies. Moreover, the disease also appeared in colonies of the Experimental Farm Apiary, the equipment of which had not previously been contaminated with E.F.B. An indication of the

TABLE I — Dates of Installation and Appearance of E.F.B. in Package Bee Colonies.

	1954					1955	
Date of hiving	Apr. 13	Apr. 16	Apr. 23	Apr. 30	May 5-7	Apr. 13	May 13
Date E.F.B. noted	May 20	May 24	May 29	June 4	June 12	May 18	June 20
Time interval (days)	37	38	36	35	36-38	35	38

TABLE II — Effects of Antibiotics on European Foulbrood, 1955.

Antibiotic	No. Colony	Average No. of E.F.B. cells per comb			
		Before treatment	10 days after	20 days after	30 days after
Streptomycin	A1	50	0	0	0
	A2	50	1	0	0
	A3	50	1	1	1
	A4	30	0	1	0
	A5	20	0	0	1
	A6	25	0	0	0
Oxytetracycline	B1	7	0	1	1
	B2	30	1	1	1
	B3	13	0	0	1
	B4	25	0	0	0
Erythromycin	C1	25	0	0	0
	C2	50	0	0	0
	C3	50	0	0	0
	C4	50	1	1	1
	C5	15	0	0	0
	C6	25	0	0	1
	C7	25	0	0	0
	C8	50	1	0	1
Chlortetracycline	D1	25	6	5	
	D2	50	7	30	
	D3	40	2	2	
	D4	10	25	20	
	D5	7	1	6	
	D6	7	3	8	
Puromycin	E1	7	50	0*	
	E2	20	7	30	
	E3	8	15	13	
	E4	5	1	1	
	E5	50	17	20	
			15 days after		
Cycloserine	F1	5	7		
	F2	13	4		
	F3	9	17		
	F4	10	10		
	F5	12	15		
	F6	20	4		

\*Queenless, no larvae.

rapid spread of E.F.B. was illustrated by one colony where the incidence of the disease increased from 10 diseased larvae to over 400 in three days.

In 1954 diseased colonies were treated with oxytetracycline and streptomycin. The antibiotics were administered in sugar-syrup by feeding or spraying on comb, or were mixed with icing sugar and dusted over the tops of the frames. The results of these tests confirmed those of other workers which showed that these antibiotics would control E.F.B. There was no difference in effectiveness by the method of treatment, whether in sugar-syrup as feed, spraying on combs, or dusting with icing sugar.

In 1955, erythromycin, chlortetracycline, cycloserine and puromycin, were tested in addition to oxytetracycline and streptomycin<sup>1</sup>. Thirty-five diseased colonies were employed in the experiment. Counts of diseased larvae were taken prior to treatment. Each colony received 250 milligrams of an antibiotic in approximately one-third gallon (1.54 litres) of 50 per cent sugar-syrup. Examinations were made at 10, 20 and 30 days thereafter for streptomycin-, oxytetracycline- and erythromycin-treated colonies; 10 and 20 days for the colonies given puromycin; and 15 days for the colonies treated with cycloserine. Data obtained are presented in Table II.

Results showed that erythromycin controlled E.F.B. in diseased colonies as effectively as streptomycin and oxytetracycline. However, the disease was not eliminated completely by these antibiotics as a few infected cells were still found in some of the colonies even after 30 days. Chlortetracycline, although it appeared to reduce E.F.B. in colonies D1 and D3, did not check the disease in the others, and therefore is not considered effective. Cycloserine and puromycin also were not effective. Puromycin at the amount given indicated some toxicity to both adults and larvae.

#### PREVENTION OF E.F.B.

In 1954 five healthy colonies were placed in an apiary where E.F.B. was present. These colonies were given a preventive treatment of 250 milligrams of oxytetracycline in sugar syrup. Examinations were made at 10-day intervals thereafter. Over a period of 40 days these colonies did not show any symptoms of E.F.B.

In 1955, approximately four weeks after hiving, 750 colonies were given a preventive treatment of 250 milligrams oxytetracycline and 150 colonies were administered 250 milligrams of streptomycin. After four weeks all colonies were examined and there was no evidence of the disease. Two weeks later a further examination was made by the commercial beekeeper. He reported a total of twenty-five colonies treated with oxytetracycline and streptomycin showed E.F.B. symptoms. Samples of dead larvae, examined microscopically, corroborated the findings. Thus, this preventive treatment of 250 milligrams of either oxytetracycline or streptomycin ensured complete protection to colonies for at least four weeks.

#### GENERAL DISCUSSION

The experimental data indicate that streptomycin, oxytetracycline and erythromycin will control E.F.B. Cycloserine, chlortetracycline and puromycin were not effective.

As the disease was not evident in the package colonies until five weeks after they were installed, preventive treatment prior to this date is suggested. Manifestations of E.F.B. were noted in packages installed in equipment at the Experimental Farm Apiary which had no previous record of this disease. It is probable, therefore, that the package bees were "carriers" of the causal organism(s) of E.F.B.

Control and preventive treatments using a dosage of 250 milligrams were effective for a period of four weeks.

It would appear from the results obtained in 1954 and 1955 that preventive treatments should commence within four weeks after installation with subsequent treatments at four-week intervals. For packages arriving in April it may be necessary to give three treatments, while for those received in May, two such treatments would probably be sufficient.

<sup>1</sup>Trade names of antibiotics used: erythromycin — erythrocin; oxytetracycline — terramycin; cycloserine — seromycin; chlortetracycline — aureomycin.

The testing of other antibiotics is continuing and preliminary trials in 1956 show that tetracycline (achromycin) is also effective against E.F.B. Observations in 1956 seem to indicate that E.F.B. may appear in package bee colonies four weeks after being installed in equipment that had been contaminated the previous year.

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# AUTHOR INDEX FOR VOLUME 4<sup>1</sup>

Abarca, Miguel . . . . .	827	Chauvin, R. . . . .	1057
Alam, S. Mashhood . . . . .	879	Clancy, D. W. . . . .	597
Allen, H. W. . . . .	743	Clark, R. C. . . . .	807
Allen, Richard K. . . . .	391	Clausen, C. P. . . . .	443
Amaro, J. P. P. . . . .	17	Collins, D. L. . . . .	335
Anderson, N. H. . . . .	659	Collyer, Elsie . . . . .	623
Angus, T. A. . . . .	711	Connola, D. P. . . . .	335
Armitage, H. M. . . . .	89	Cortés Iturbe, Alfonso . . . . .	827
Atwal, A. S. . . . .	889	Cory, Ernest N. . . . .	841
Austin, G. H. . . . .	1001, 1059	Cotton, R. T. . . . .	81
Baeta Neves, C. M. . . . .	17, 251	Crooke, Myles . . . . .	233
Baird, A. B. . . . .	483	Crosby, David . . . . .	823
Baird, Ronald B. . . . .	689	DeBach, Paul . . . . .	759
Baker, W. A. . . . .	487	de Fluiter (see Fluiter)	
Balch, R. E. . . . .	807	Delucchi, V. L. . . . .	891
Banks, C. J. . . . .	907	Dove, Walter E. . . . .	65
Barnes, Douglas . . . . .	19	Dowden, Philip B. . . . .	823
Beal, James A. . . . .	323	Dunham, W. E. . . . .	926
Berck, B. . . . .	99	Dustan, G. G. . . . .	493
Bergold, G. H. . . . .	442	Easter, Stephen S. . . . .	51
Bess, Henry A. . . . .	543, 835	Eckert, John E. . . . .	991
Bickley, William E. . . . .	841	Edmunds, George F., Jr. . . . .	391
Biliotti, E. . . . .	751	Elton, E. T. G. . . . .	573
Bird, F. T. . . . .	687	Ewan, Herbert G. . . . .	363
Bletchly, J. D. . . . .	385	Fettes, James J. . . . .	281
Blunck, Hans . . . . .	703	Flanders, S. E. . . . .	579
Boettger, Caesar R. . . . .	875	Fleschner, C. A. . . . .	627
Bohart, George E. . . . .	929	Flieger, B. W. . . . .	185
Bongberg, J. W. . . . .	193	Flores Caceres, Silverio . . . . .	827
Bovey, Paul . . . . .	123	Fluiter, H. J. de . . . . .	603
Boyce, H. R. . . . .	493	Fonseca (see Cancela da Fonseca)	
Braun, E. . . . .	927	Franz, Jost M. . . . .	461, 781
Briggs, John D. . . . .	723	Freeman, J. A. . . . .	5
Brower, A. E. . . . .	205	Fullaway, David T. . . . .	549
Brown, N. R. . . . .	807	Gardner, T. R. . . . .	465
Brown, R. C. . . . .	247	Gibson, D. R. . . . .	927
Bucher, G. E. . . . .	695	Gochner, Thomas A. . . . .	1091
Buckner, C. H. . . . .	353	Goldsmith, E. D. . . . .	442
Butovitsch, V. . . . .	275	Gösswald, K. . . . .	567
Caceres (see Flores Caceres)		Gradwell, G. R. . . . .	133
Cachan, Pierre . . . . .	393	Graham, Samuel A. . . . .	261
Cancela da Fonseca, J. P. . . . .	17		
Chant, D. A. . . . .	649		
Chapman, J. A. . . . .	375		

<sup>1</sup> See Volume 1 for author index to all volumes.



- Green, G. W. . . . . 373  
 Greenbank, D. O. . . . . 137  
 Grison, Pierre. . . . . 442, 675  
 Guido (see Silveira Guido)  
  
 Hall, Ralph C. . . . . 341  
 Haramoto, Frank H. . . . . 543, 835  
 Hassett, Charles C. . . . . 47  
 Haydak, Mykola H. . . . . 1053, 1079  
 Heimpel, A. M. . . . . 711  
 Herbert, H. J. . . . . 617  
 Herne, D. C. . . . . 667  
 Hitchcock, John D. . . . . 1097  
 Hobbs, G. A. . . . . 939  
 Holdaway, F. G. . . . . 943  
 Holling, C. S. . . . . 351  
 Holloway, James K. . . . . 557  
 Howe, R. W. . . . . 23  
 Howitt, Angus J. . . . . 895  
 Huffaker, C. B. . . . . 533  
 Husson, Roger . . . . . 437  
  
 Inouye, Motonori. . . . . 163  
 Iturbe (see Cortés Iturbe)  
 Ives, W. G. H. . . . . 407  
 Iyatomi, Kisabu. . . . . 897  
  
 Jamieson, C. A. . . . . 1059, 1109  
 Jaynes, H. A. . . . . 585  
 Johnston, H. R. . . . . 423  
 Jones, Luther G. . . . . 967  
 Jones, Tecwyn. . . . . 381  
  
 Kaloyereas, Socrates A. . . . . 1007  
 Karmo, E. A. . . . . 955  
 Katznelson, H. . . . . 1105  
 Keen, F. P. . . . . 171  
 Khan, M. A. . . . . 873  
 Knierim, John A. . . . . 926  
 Kowal, R. J. . . . . 399  
 Kraus, Manfred. . . . . 797  
 Krieg, A. . . . . 737  
 Kuenen, D. J. . . . . 611  
  
 La Huë, D. W. . . . . 77  
 Laidlaw, Harry H., Jr. . . . . 1067  
 Laird, Marshall. . . . . 901  
 Langford, George S. . . . . 841  
 Laudani, Hamilton. . . . . 35  
  
 Levin, Marshall D. . . . . 1079  
 Löken, Astrid. . . . . 961  
 Lord, F. T. . . . . 617  
 Luitjes, J. . . . . 201  
  
 MacPhee, A. W. . . . . 617  
 MacVicar, R. M. . . . . 927  
 Marsh, George L. . . . . 991  
 Mashhood Alam (see Alam)  
 Massee, A. M. . . . . 623  
 Mathys, G. . . . . 607  
 Maurizio, A. . . . . 1025  
 McAlister, H. J. . . . . 597  
 McGugan, B. M. . . . . 219  
 McIntyre, T. . . . . 369  
 Medler, J. T. . . . . 973  
 Mesnil, L. P. . . . . 777  
 Michael, A. S. . . . . 1089  
 Miller, C. A. . . . . 137  
 Milner, Max. . . . . 45  
 Milum, V. G. . . . . 1085  
 Monteith, L. G. . . . . 769  
 Morgan, C. V. G. . . . . 659  
 Morris, R. F. . . . . 137  
 Morse, Roger A. . . . . 951  
 Mott, D. G. . . . . 137  
 Muma, Martin H. . . . . 633  
  
 Neves (see Baeta Neves)  
  
 Oertel, E. . . . . 1007, 1027  
  
 Pankiw, P. . . . . 927, 1109  
 Parker, Ralph L. . . . . 1037  
 Parkin, E. A. . . . . 57  
 Pedersen, M. W. . . . . 1019  
 Pengelly, David H. . . . . 945  
 Pereira Amaro (see Amaro)  
 Plus, N. . . . . 741  
 Popov, V. B. . . . . 983  
 Post, A. . . . . 611  
 Pschorn-Walcher, Hubert. . 795, 797, 801  
 Putman, Wm. L. . . . . 667  
  
 Rashad, Salah El-Din. . . . . 1037  
 Rawlings, G. B. . . . . 241  
 Reddy, D. Bap. . . . . 349  
 Robert, Adrien. . . . . 433

- |                              |          |                             |            |
|------------------------------|----------|-----------------------------|------------|
| Roonwal, M. L.....           | 317      | van de Vrie, (see Vrie)     |            |
| Ruffinelli, Agustín.....     | 913      | Varley, G. C.....           | 133        |
| Sandner, Henryk.....         | 471      | Voûte, A. D.....            | 109, 201   |
| Scaramuzza, L. C.....        | 845      | Vrie, M. van de.....        | 603        |
| Schade, John.....            | 991      | Walkden, H. H.....          | 45         |
| Schwenke, Wolfgang.....      | 851      | Warren, Lloyd O.....        | 29         |
| Schwerdtfeger, F.....        | 115      | Watanabe, Chihisa.....      | 515        |
| Shuel, R. W.....             | 1017     | Watters, F. L.....          | 105        |
| Silveira Guido, Aquiles..... | 913      | Way, M. J.....              | 595, 907   |
| Simmonds, F. J.....          | 475, 553 | Weaver, Nevin.....          | 1031, 1065 |
| Smirnoff, W. A.....          | 903      | Webb, F. E.....             | 303        |
| Smit, Bernard.....           | 911      | Webb, W. E.....             | 381        |
| Smith, B. C.....             | 819      | Weiser, Jaroslav.....       | 681        |
| Smith, J. Morris.....        | 561      | Welch, Harold E.....        | 863        |
| Smith, M. V.....             | 1063     | White, Jonathan W., Jr..... | 1015       |
| Spear, P. J.....             | 49       | Whiteside, J. M.....        | 291        |
| Spencer, G. J.....           | 497, 503 | Wilbur, Donald A.....       | 29, 73     |
| Stark, R. W.....             | 151      | Wille, J. E.....            | 519        |
| Steinhaus, Edward A.....     | 725      | Wolcott, George N.....      | 417, 511   |
| Steyn, J. J.....             | 589      | Womersley, J. S.....        | 331        |
| Stute, Karl.....             | 1047     | Wygant, N. D.....           | 181        |
| Sweetman, Harvey L.....      | 449      | Wylie, H. G.....            | 789        |
| Szent-Ivany, J. J. H.....    | 331      |                             |            |
| Tadić, Milorad D.....        | 855, 859 | Yamafuji, Kazuo.....        | 731        |
| Tenhet, J. N.....            | 87       | Yasumatsu, Keizô.....       | 771        |
| Thompson, Clarence G.....    | 693      |                             |            |
| Thompson, W. R.....          | 479      | Zacher, Friedrich.....      | 33         |
| Tothill, J. D.....           | 525      | Zwölfer, Helmut.....        | 795, 869   |
| Townsend, G. F.....          | 971      | Zwölfer, W.....             | 209        |

























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